The Effects of Gaze Control and Body Segment Recoupling on Human Gait and Foot Pressure Variability: A Modern and Evolutionary Perspective

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by

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Dedicated to the Memory of my Beloved Grandmother

Elsie May Webster

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“Unable are the loved to die. For love is immortality.”

Emily Dickinson

And also

Mum, Dad, and Ashley

With All my Love Always

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Abstract

This thesis investigates the relationships between gaze control, body segment coupling, and foot pressure patterns during walking, and discusses the resulting implications for both modern humans and our evolution. One of the major changes thought to underlie the transition between *Australopithecus* and *Homo* is the decoupling of the head and shoulders, and trunk and hips. The independent rotation of these segments enables greater control of the torque and free moments resulting from leg swing, and is considered key in the control of bipedal locomotion. Fossil evidence of semicircular canal morphology (Spoor et al., 1994) also indicates congruent changes in the vestibular system, which alongside the ability to track moving objects with clarity using smooth pursuit eye movements, are likely to have been fundamental to sensory integration and prioritisation during locomotion.

This research therefore assesses how the increased neurological demands of active visual tracking in environments of varying visual complexity, and the artificial recoupling of body segments, impact on foot pressure variability during locomotion in modern man. The results demonstrate that foot pressure variability appears unaffected by larger levels of background visual clutter when tracking using smooth pursuit eye movements - variability appears to be higher in very low levels of visual clutter when there is a relative absence of visual referents. This variability was found to further increase when undertaking a secondary auditory task whilst compared to visual tracking alone. When considering the effects of experimental recoupling of body segments, an increase in foot pressure variability was also observed when compared to natural unrestricted walking, with increased arm and leg swing appearing to compensate for reduced hip and shoulder rotations.

These changes in foot pressure variability indicate less consistent gait patterns, and suggest the utilisation of postural correction mechanisms, such as the lateral ankle strategy, to remain stable. The normal ageing process, and resulting joint stiffness and visual, vestibular, and cognitive decline, may

be expected to exacerbate such variability increasing the likelihood of falls. This research therefore not only contributes to the understanding of potential locomotor strategies in early hominins, but also has significant implications for the safety of the elderly and infirm during locomotion, particularly with respect to the built environment.

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List of Abbreviations

*	$p \leq 0.05$
**	$p \leq 0.01$
ANOVA	Analysis of Variance
c.	Circa
cc	Cubic Centimetres
CNS	Central Nervous System
Ka	Thousand Years Ago
Ma	Million Years Ago
m/s^{-1}	Metres per Second
ms	Milliseconds
N/cm^2	Newtons per centimetre
pSPM	Pedobarographic Statistical Parametric Mapping

1 Introduction

1.1 Postural Control in Modern Humans

Postural control can be defined as the control of the position of the body in space in order to maintain stability and orientation (Shumway-Cook and Woollacott, 2000b). In this respect, orientation refers to the relationship between the segments of the body, and also the relationship between the body and the environment (Horak and Macpherson, 1996). Stability, or balance, refers to the ability to maintain the body in equilibrium: in other words, its movement is not significantly altered from the desired trajectory.

The maintenance of postural control therefore requires the integration of the central nervous system, musculoskeletal system, and sensory systems in order to generate an appropriate motor response. The highly complex interactions between these systems can be broken down into seven components to build a model of the postural control system (Cech and Martin, 2012). This includes limits of stability, sensory organisation, eye-head stabilisation, the musculoskeletal system, motor coordination, predictive central set, and environmental adaptation.

The perimeters of the base of support define the typical ***limits of stability***. When body weight is maintained above the base of support (Shumway-Cook and Woollacott, 2000b) i.e. the centre of the body's total mass is balanced above the area of the body in contact with the ground, posture can be maintained. Different postures have a different base of support. During quiet stance for example, the circumference of the circular area defined by anterior-posterior and medio-lateral sway over the ankles can be thought of as a 'cone of stability' which represents the limits within which standing posture can be maintained (Martin and Kessler, 2000).

Sensory organisation is a critical component of the postural control system, with the visual, vestibular, and somatosensory systems essential in providing information regarding movement of the body and its position in space

in order to cue appropriate postural responses. Somatosensation, the combined sensory inputs of touch and proprioception (McKeon and Hertel, 2007), provides information from the lower limbs with regard to changes in pressure distribution under the feet (McKeon and Hertel, 2007), the length and tension of muscles, and activity at the ankle joint (Bray et al., 1999). The visual and vestibular systems are also crucial in providing information regarding movement of the environment and the head respectively. As the eyes must be able to maintain stability of the visual scene at all times, including as the head moves, the two act concurrently to ensure ***eye-head stabilisation*** so that vision is accurate and the head is stable in space (Cech and Martin, 2012). The importance and integration of all of the above senses is explored in more detail in chapter 1.3.

The ***musculoskeletal system*** is a highly complex mechanically linked system containing many muscles, joint, tendons, and ligaments. Normal muscle tone, the force with which a muscle resists being lengthened, is naturally present, and many muscles of the body are tonically active during quiet stance (Basmajian and De Luca, 1985). This includes the soleus and gastrocnemius since the line of gravity falls slightly forwards of the knee and ankle, and the thoracic erector spinae of the trunk because the line of gravity falls forwards of the spinal column (Basmajian and De Luca, 1985). As such, ***motor coordination*** is key in coordinating the appropriate activation of such muscles to preserve posture. This includes the use of muscle synergies, a functional coupling of a combination of muscles such that they act together as a unit, hence reducing the demands on the central nervous system (Shumway-Cook and Woollacott, 2000b). It also includes specific locomotor strategies aimed at maximising balance. Examples of both of which are described in chapter 1.4 below.

Such motor synergies can also be guided by the ***predictive central set***. This internal representation of the dynamics of specific movements can be utilised as a guide to prepare an appropriate response (Horak et al., 1989), for example when catching or throwing an object, or sitting or rising from a chair.

All of these factors of course ultimately depend on the exact environment and task at hand, and hence ***environmental adaptation*** is also an important component of postural control. For instance, if one sense is not providing accurate information regarding the position and movement of the body, then the input of the other senses will become more important (Horak and Macpherson, 1996). For example, somatosensory information will be less reliable on slippery or unstable surfaces, and therefore visual and vestibular information is likely to be more heavily relied on.

1.2 Types of Postural Control

Within this postural control system, four types of postural control have been defined: static, reactive, and anticipatory and adaptive postural control. ***Static*** postural control refers to the maintenance of the body's centre of mass within the limits of the base of support (Shumway-Cook and Woollacott, 2000b). During quiet standing, postural control is considered static, although static posture in itself involves a natural degree of sway over the ankles as we maintain balance.

Reactive postural control compensates for unexpected perturbations to the centre of mass that might place it outside the base of support (Nashner, 1980). Depending on the magnitude of the perturbation, different postural movement responses are produced in response to the perturbation (Horak and Nashner, 1986). For example if the centre of mass was to be displaced to the left due to a slip, the weight shift over the left foot would be detected and automatic postural responses adjust posture to bring the centre of mass back to the right and into alignment with the base of support.

Anticipatory postural control includes postural adjustments that are made in anticipation of an upcoming task. In these instances, the central nervous system forms a sensorimotor plan for the actions required based on prior experience of similar tasks (Shumway-Cook and Woollacott, 2000b). For

example, when planning to lift a heavy object we are aware of the load from prior experience, and hence can prepare our posture to be able to cope accordingly. In order to do this, information regarding the upcoming event based on past experiences is fed forward to the muscles involved in controlling posture and load distribution through the predictive central set to enable them to prepare for the action.

Finally, ***adaptive*** postural control allows for changes to be made to posture in response to current need (Cech and Martin, 2012), for example during environmental adaptation as described above.

The maintenance of stability therefore requires a delicate balance of systems to maintain a constant position of the centre of mass and minimise its displacement (McCollum and Leen, 1989). The vertical projection of such forces is known as the centre of pressure. The net centre of pressure lies between the feet during double support; however there is also a separate underfoot centre of pressure for each foot (Winter, 1995). Analysing the path of the underfoot centre of pressure can therefore provide considerable insight into how the body has maintained stability; for instance through the relocation of the centre of mass by coordinated movement of different body segments.

1.3 Sensory Inputs and Postural Control

1.3.1 Visuo-vestibular

Visual and vestibular inputs provide information about the position of the head relative to the environment. During locomotion, the eyes can be subjected to changing acceleration within a step cycle resulting in considerable vertical linear translation and rotations of the head. This occurs during natural locomotion on the ground and in treadmill experiments (Moore et al., 1999). Acceleration of the head is attenuated to about 23% of the horizontal acceleration of the hip in young, healthy adults (Winter, 1991), and stabilisation of the head with respect to the environment has been shown to be precise during walking, and even running and hopping (Pozzo et al., 1990). By

restricting angular motions of the head, the ocular compensation required to maintain gaze stabilisation is also reduced. Thus, the body is able to maintain both balance and visual acuity during locomotion in a complex environment.

The importance of visual information in the control of standing balance has been known for many years, with the increased magnitude of postural sway observed when the eyes are closed argued to demonstrate the importance of visual inputs (Lee and Lishman, 1975, Edwards, 1946). However, more recently vision has been shown to take on an even greater role during locomotion due to the clear need to avoid obstacles and navigate safely (Grasso et al., 1998, Patla and Vickers, 1997). It therefore appears that by utilising information from 'optic flow' - the pattern of perceived motion of objects, edges, and surfaces in the visual field (Gibson, 1954) - gait characteristics such as speed (Konczak, 1994) and stride length (Prokop et al., 1997) are appropriately modulated for a situation or task at hand. Indeed, vision is the only sensory modality that can provide information concerning distant environmental features – hence, it can be used in a feedforward manner to make postural adjustments for upcoming obstacles and changes in direction (Hollands et al., 2002). This predictive and anticipatory role has been demonstrated in several situations, for example when making anticipatory eye movements prior to making a turn (Grasso et al., 1998), and when approaching (but not when stepping over) an obstacle (Patla and Vickers, 1997).

To be able to make such anticipatory adjustments however, the visual input has to be highly accurate. Therefore, in order to maintain visual acuity, a variety of volitional and reflexive eye movements are employed in order to track objects of interest and stabilize gaze upon them. The reflexive eye movements are the phylogenetically oldest and evolved in order to focus objects of interest on the retina as a whole. This includes the vestibulo-ocular reflex. The role of the vestibulo-ocular reflex is to generate compensatory eye movements in response to head movements, and thereby maintain a stable image and preserve visual acuity (Paige and Seidman, 1999). To achieve this, the

vestibulo-ocular reflex consists of components that compensate for both translational and rotational motions of the head. The translational vestibulo-ocular reflex is the phylogenetically younger of the two reflexes, and is only well described for humans and primates (Liao et al., 2010, Angelaki et al., 2000, McHenry and Angelaki, 2000). It is generally considered that the functional goal of the translational vestibulo-ocular reflex is to reduce retinal image slip, and reduce binocular disparities occurring in self-motion (Hess and Angelaki, 2003, McHenry and Angelaki, 2000).

Unlike the translational vestibulo-ocular reflex, The rotational vestibulo-ocular reflex is highly conserved throughout evolution (Angelaki, 2004), and is called upon to stabilise the whole of the visual field on the retina during head rotations by rotating the eyes in parallel with the axis of head rotation.

The optokinetic reflex is another highly conserved primitive motion sensing reflex that maintains a constant retinal position for images during movement. The optokinetic reflex can be observed in the majority of vertebrates with a mobile head or eyes (Huang and Neuhauss, 2008, Walls, 1962) and also in some invertebrates (Land, 1999). However, as it occurs over the entire retina, there is a resultant lack of visual acuity; thus it cannot provide information as to object identity. In humans the response is dominated by the more recently acquired fast optokinetic reflex (Cohen et al., 1981). The fast optokinetic reflex is closely associated with smooth pursuit eye movements (Barnes, 1993), the higher gain of which enables much more effective retinal image stabilisation (see below).

Other volitional eye movements evolved with the evolution of the fovea, the area of the retina where acuity is greatest (Carpenter, 1988), in order to extract more detailed information regarding the environment. The fovea is extremely small, with an angular diameter of just 0.3 and 2°; thus, the foveal depression only accounts for 1/4000th of the retinal surface (Steinman, 2003). Hence the maintenance of an image on the fovea requires complex oculomotor control. Saccades are rapid step-like movements of the eye that redirect the

fovea to an object of interest, and hence ensure high clarity (Carpenter, 1988). As saccadic movements are not entirely accurate at about 5-10% of saccadic amplitude (Kowler and Blaser, 1995), they are often very quickly supplemented by smaller corrective saccades to ensure that the object is fully fixated. Furthermore, even when the eyes are fixed on the target, microsaccades of less than 0.5 degrees ensure that visual perception does not fade (Martinez-Conde et al., 2000)

Saccadic movements are also a vital component of smooth pursuit eye movements. These smooth pursuit movements are essential in order to maintain moving objects on the fovea, and enable the eye to track moving targets smoothly and with clarity (Carpenter, 1988). When compared to saccadic movements, which are known to reach velocities of up to 700°/s (Carpenter, 1988), smooth pursuit eye movements are much slower (Robinson, 1981) initiating around 90-150ms after target movement (Rashbass, 1961). As a result of this latency, the point of eye fixation is left lagging behind the target despite the fact that eye and target velocity are matched. Consequently, without an initial saccadic component driven by target offset, smooth pursuit eye movements are unable to centralise the target image on the fovea. Indeed, smooth pursuit will only work alone for target velocities up to 15°/s, beyond which it must be supplemented by saccades. For target movements greater than 100°/s, pursuit movements are entirely saccadic (Land, 2006). It has been known for some time that smooth pursuit eye movements can be influenced by learning, and hence are subject to predictive components. For example, studies have demonstrated that after repeated presentation of a moving target, when followed by a presentation in which the trajectory is unexpectedly changed, smooth pursuit eye movements continue along the path of the previous movement of the target until the conflict has been registered (Barnes and Asselman, 1991).

1.3.2 Somatosensation

Visual and vestibular inputs are also supplemented by somatosensation which includes both the tactile and proprioceptive systems (McKeon and Hertel, 2007). The tactile system is associated with the senses of touch, vibration, and pressure, detected by mechanoreceptors including Merkels cells, Pacinian Corpuscles, Meissner's Corpuscles, and Ruffini endings (Bray et al., 1999). As these cutaneous receptors are found within the feet, and hence are found at the interface between the body and the ground, they are considered important in the control of upright posture (Kavounoudias et al., 1998). Indeed, studies that have attempted to disrupt feedback from such receptors have demonstrated their contribution to the control of balance: for instance, research has shown that when vibration is applied to the soles of the feet during standing that involuntary whole body tilt is induced (Kavounoudias et al., 1998). Furthermore, studies have shown similar effects when cooling (McKeon and Hertel, 2007) or anaesthetising (Meyer et al., 2004) the receptors on the soles of the feet, reporting an observed decrease in postural stability.

Proprioceptive inputs include the sensations of changes in muscle length, muscle tension, and joint angles (McKeon and Hertel, 2007), and are measured by muscle spindles, joint afferents and Golgi tendon organs (McKeon and Hertel, 2007). Proprioceptive inputs provide feedback that is considered critical for automatic balance responses (Van Deursen and Simoneau, 1999, Kavounoudias et al., 1998): for example receptors in the legs provide information that can maintain posture via strategies discussed in more detail in chapter 1.4.

The importance of somatosensation to such postural control mechanisms is highlighted both when it is reduced and increased: for example, in neuropathy a decline in balance control is observed (Van Deursen and Simoneau, 1999), whereas light fingertip touch to a stable surface is sufficient to reduce postural sway (Jeka and Lackner, 1994).

1.4 Motor Mechanisms for Postural Control

1.4.1 Reflexes and Muscle Synergies

Thus, after sensory inputs have been weighted depending on the environment, a range of automatic motor responses are generated to maintain balance. Inputs from the visual, vestibular, and somatosensory systems all influence 'postural tone': that is, the background activity of antigravity muscles that ensure the maintenance and fine-tuning of upright posture (Shumway-Cook and Woollacott, 2000b). For example, for continual fine tuning of posture, the vestibular inputs alter the distribution of postural tone in the neck and limbs in order to stabilise the head, and by association stabilise gaze.

This is achieved by two reflexes, the vestibulo-spinal reflex and the vestibulo-collic reflex (Massion and Woollacott, 1996). The vestibulo-spinal reflex consists of two sub-pathways, the lateral vestibulo-spinal tract and the medial vestibulo-spinal tract. The former stabilises upright posture through innervation of the extensor muscle of the legs (Pompeiano, 1972); the latter stabilises the position of the head in space through mediation of the vestibulo-collic reflex (Wilson and Schor, 1999, Iwamoto et al., 1996). Further, the somatosensory inputs in the neck also contribute to head stabilisation. The afferent sensory changes caused by changing neck position generate compensatory contractions though the cervico-collic reflex (Goldberg and Peterson, 1986) in order to stabilise the head on the body.

However, when the centre of mass is subject to a larger perturbation, the actions of motor synergies are required to correct balance. For smaller disturbances to the centre of mass, 'in-place' strategies can be employed immediately during the same step in which the disturbance has taken place, and hence can quickly correct imbalance. One such strategy is the ankle strategy, historically, one of the first patterns for the control of anterior-posterior sway to be identified. It has been known for some time that through movement centred around the ankle joint, the muscles of the ankle, knee, and hip act

synergistically to correct for anterior-posterior instability (Nashner, 1977). Following detection of forward sway perturbation through somatosensory receptors in the legs and feet, activation of the gastrocnemius occurs at around 100 ms producing a torque to slow and reverse the forwards acceleration, which is then followed by activation of the hamstrings and paraspinal muscles to extend the hip and knees (Horak and Nashner, 1986). In response to backwards sway, the anterior tibialis is activated first, followed by the quadriceps and finally the abdominals. More recently, a lateral ankle strategy has also been proposed in which modulation of foot rollover is argued to be important in helping to quickly regain centre of mass stabilisation during medio-lateral perturbations, but also in fine-tuning through compensating for inaccurate foot placement (Hof et al., 2010). Another strategy that can be used in-place is the hip strategy (Horak and Nashner, 1986). Use of ankle strategies requires force generation in the muscles of the ankle joint and is most effective when on a stable support surface and the perturbation is small (Shumway-Cook and Woollacott, 2000b)

Another strategy that may be employed to counteract anterior-posterior imbalance is the hip strategy. The hip strategy produces large and rapid counter-acting motion at the hip, and may be implemented when perturbations are faster or larger or occur on unstable supports (Horak and Nashner, 1986). To counteract forward sway, the abdominals are first activated followed by the quadriceps. In instances of backwards sway, the paraspinal muscles are first activated followed by the hamstrings (Horak and Nashner, 1986). Both muscle synergies bring the centre of mass back into alignment with the base of support.

However, when in-place strategies are insufficient in maintaining balance, the only solution is to correct at the next step. By taking a step, the support base can be realigned under the centre of mass, thus the stepping strategy is therefore used during particularly large perturbations that move the centre of mass out of the base of support (Nashner, 1989). That said, stepping responses have also been observed in situations where the centre of mass is still within the

base of support and before the limits of stability are reached (Brown et al., 1999, McIlroy and Maki, 1993).

1.4.2 Human Gait and Balance Adaptations

Various combinations of the afore-mentioned strategies are used during standing posture, depending upon the boundaries in which they can safely be used (Horak and Nashner, 1986). However, balance is yet further compromised during locomotion. During 40% of the gait cycle the body's weight is borne by entirely by one supporting limb (Sutherland et al., 1994), and hence the stabilisation of the body over the one limb in contact with the ground is critical to balance. A delicate balance of forces is therefore required to maintain a constant position of the centre of mass and minimise its displacement (McCollum and Leen, 1989). The vertical projection of such forces is known as the centre of pressure. The net centre of pressure lies between the feet during double support; however there is also a separate underfoot centre of pressure for each foot (Winter, 1995). Analysing the path of underfoot pressures can therefore provide considerable insight into how the body has maintained stability.

As well as the aforementioned motor synergies responsible for the ankle, hip, and stepping strategies, several aspects of the human gait pattern help maintain the centre of pressure and preserve balance during locomotion. This is particularly the case during rotation of the pelvis as the swing leg induces a destabilising torque in what is known as the 'pelvic step' (Ducroquet et al., 1968). In order to counteract this, an opposing axial counter-rotation of the trunk acts to reduce angular momentum about the longitudinal axis (Gracovetsky, 1985). To compensate, these forces must be offset by equal opposing torques generation of counter-rotations of the trunk. As such, derived structural modifications enable the independent counter-rotation of the body segments to produce these balancing torques, including the presence of a narrow elongated waist (Aiello and Dean, 1990) that separates the trunk from the pelvis.

There is, however, debate as to whether these counter-rotations are advantageous at walking speeds. Bramble and Lieberman (2004) suggest that the benefits of the decoupling of body segments are linked only to running as they enable the control of destabilising torques in the aerial phase. They argue that during walking, the actions of the abductors and medial rotators of the hip of the stance leg are sufficient to control the inertially-induced rotation of the trunk. Conversely, there is evidence to suggest the recruitment of counter-rotations at walking speeds (Witte et al., 2004), and that axial rotation of the thorax increases with walking velocity (Feipel et al., 2001). This would suggest that although trunk rotations may be especially important at higher speeds, they are nonetheless advantageous during walking. Further, the lumbar lordosis of the spine enables flexion and extension of the trunk, and also absorbs body weight (Lovejoy, 2005). As the vertebrae also increase in mass caudally (Haeusler et al., 2002), this provides further adaptation to load-bearing.

Trunk counter-rotations are also aided by arm swing, the importance of which has been demonstrated both in terms of balance and energetic efficiency (Pontzer et al., 2009b, Li et al., 2001). This dual benefit of arm swing is a consequence of its active and passive components. Passive arm swing is driven by trunk rotation and the passive mass damper effect of the shoulders (Pontzer et al., 2009), thereby balancing the angular momentum produced by leg swing with minimal energetic input. However, if balance is threatened the passive component of arm swing may not be sufficient to maintain stability. Therefore, active arm swing is employed in order to increase the counter-torsional effects of arm swing when the passive component alone is insufficient (Pontzer et al., 2009). The effects of arm swing in reducing destabilising torques are increased by the broadness of the shoulders (Bramble and Lieberman, 2004).

Several features of the lower body also contribute to balance control, with the pelvis and lower limb modelled to allow for efficient forward propulsion whilst maintaining the balance of the upright trunk (Harcourt-Smith, 2007). The short, wide iliac blades and wide sacrum of the pelvis place the centre of gravity of the

trunk closer to the hip and position the lesser gluteal muscles at the side of the pelvis (Lovejoy, 1988). The result is that the trunk is able to tilt towards the supporting leg, providing greater stability and balance. Adaptations to high loads associated with bipedal posture are also seen in the lower limb, with large joints relative to body size (Jungers, 1988). Further, the high bicondylar angle of the femur (8-11°) (Aiello and Dean, 1990), positions the knee close to the body midline and thus helps balance the centre of mass above the base of support.

1.5 Adaptive Postural Control: Effects of Sensory Load and Attention

In order to be able to respond effectively to changes in the relationships between the body and the position of the surrounding objects in space, signals from all three sensory systems: visual, vestibular, and somatosensory must be integrated. As no one sense alone can provide accurate information regarding the movement of the body in space, the central nervous system must organise sensory inputs to generate the appropriate motor strategies for the conditions and task at hand.

It is in the parietal cortex where visual and vestibular information is integrated with that of the somatosensory system. In particular the inferior parietal lobule in Brodmann area 7 is heavily involved in the analysis and integration of higher order multi-modal integration. Neurons in area 7 process both body-referenced and world-referenced signals, and can hence provide an accurate image of the body's position in space (Lynch, 1980). Indeed, the inferior parietal lobule is considered to act as a sensorimotor interface at which goal-directed motor actions are organised and planned (Fogassi and Luppino, 2005).

Exact motor responses are of course dependent on the environment and task at hand, and the CNS must continually adjust to rely more heavily on the most appropriate and accurate information available at the time. For example when subjected to a sudden increase in optic flow across the visual field, such

as traffic moving past, stability might be threatened by the sudden visual flow if balance was to remain strongly linked to visual inputs (Logan et al., 2010). In this instance, somatosensory and vestibular inputs become more important in maintaining an accurate picture about the body's position within the environment and hence support upright equilibrium. Sensory reweighting therefore emphasises and de-emphasises sensory inputs based on the task at hand (Horak and Macpherson, 1996), in order to maintain stability. For example, the provision of tactile, visual, and auditory 'perceptual anchors' have been shown to reduce the level of postural sway induced by a visual motion stimulus (Meyer et al., 2013, Meyer et al., 2012) as postural control no longer remains heavily coupled to the moving visual stimulus.

However, despite this sensory reweighting, complex sensorimotor integration can still place considerable neurological demand on processing. Therefore, when there is conflict between postural control and other cognitive demands, motor responses must also be prioritised according to the most immediate need. The ability to prioritise tasks in this manner is controlled by executive function: the higher cognitive processes that generate and modulate behaviour based on sensory information (Lezak et al., 1995). One component of executive function is divided attention, or the ability to perform multiple tasks simultaneously (Lezak et al., 1995). The allocation of attention amongst tasks therefore impacts on how well they are performed.

Ecologically speaking, the maximisation of balance and avoidance of hazards may be considered more important than secondary cognitive tasks, and so it might be expected that more attention is allocated to postural control in most circumstances. Indeed, this is reported to be the case, with healthy subjects argued to use a 'posture first' strategy to give priority to stability over other cognitive tasks when not instructed otherwise (Shumway-Cook et al., 1997). However, others have indicated that this is not always the case, with young, healthy subjects having also been shown to allocate more attention to cognitive tasks rather than gait stability in several studies. In these instances,

secondary cognitive tasks have been shown to induce an increase in stride-to-stride variability (Taylor et al., 2013, Beauchet et al., 2005), a decrease in stride length (Simoni et al., 2013, Taylor et al., 2013, O'Shea et al., 2002), and decreased walking speed (Simoni et al., 2013, Taylor et al., 2013, O'Shea et al., 2002).

Why then might subjects allocate attention to postural control and cognitive tasks differently? The nature of the task and environment, and prior experience my go some way to explaining these differences. For example, under most circumstances, visuo-motor responses are strongly coupled to postural control for the purposes of ensuring obstacle avoidance and recognising potential threats (Grasso et al., 1998). Hence, if the subject perceives strong risk in the environment they will likely prioritise these responses over a cognitive task. For instance, when walking on a narrow elevated walkway subjects allocated more attention to postural control than a cognitive task (Gage et al., 2003). However, if the task is simple and postural threat is low, healthy subjects with ample postural reserve will likely prioritise the cognitive task for as long as they perceive it safe to do so (Yogev-Seligmann et al., 2012). It has also been shown that overlearned and skilled tasks place less demand on attention (Schmidt, 2008), and studies have shown that walking performance during dual-task scenarios can be improved with training (Silsupadol et al., 2009, Bherer et al., 2006). It is evident therefore, that the multi-modal control of posture is complex and highly dependent on the situation and complexity of task at hand.

1.6 Postural Control and Ageing

1.6.1 Sensorimotor Deficits Associated with Ageing

Although sensorimotor systems act effectively to control balance in healthy individuals, there are clear implications for the abilities of those in whom sensory and motor coordination deficits are common.

For instance, reduced visual function with ageing is known to alter eye movement control (Knox et al., 2005, Spooner et al., 1980, Sharpe and Sylvester, 1978). An increase in the latency of eye movements including smooth pursuit eye movements (Knox et al., 2005) and saccades (Munoz et al., 1998, Fischer et al., 1997, Pratt et al., 1997, Sharpe and Zackon, 1987) has been observed when compared to younger controls. As it appears that the motor circuitry responsible for eye movements is quite resistant to the effects of age (Munoz et al., 1998, Vijayashankar and Brody, 1977), but that there is a general reduction in the ability of older subjects to detect and respond to visual signals (Willis and Anderson, 2000, Porciatti et al., 1999), it has been argued that age related decline in sensory processing may be somewhat responsible for such latencies (Knox et al., 2005). It has been shown that visual decline directly contributes to falls (Abdelhafiz and Austin, 2003, Ivers et al., 2000, Grisso et al., 1991) and increased mortality (Lee et al., 2002, Appollonio et al., 1995), even in the absence of overt eye pathology. Further, estimates suggest a total of almost 756,000 people living with age-related macular degeneration in the UK by 2020 (Minassian et al., 2011), which can further intensify the risks to postural control.

Also contributing to reduced balance control is the decline of the vestibular system. Indeed, after age 40 a 3% decline in the vestibular function is seen each decade (Schwartz, 2013), and a 37% reduction in vestibular neurons has been reported in elderly subjects when compared to younger counterparts (Bergström, 1973). Furthermore, the risk of vestibular disorders such as benign paroxysmal positional vertigo increases: at least a third of elderly individuals over 70 experience a period of such vertigo at least once (Rogers, 2010).

With regards to somatosensation, the loss of vibratory sensation is reported as one of the common sensory losses in the elderly (Cech and Martin, 2012). Indeed, this has been shown to be particularly the case in the big toe (Merchut and Toleikis, 1989) which has clear implications for the amount of tactile feedback generated by mechanoreceptors of the plantar surface of the foot. The sensation of vibration has been shown to reduce after 50 years of age

(Steiness, 1957) and the threshold for detection appears to be doubled at age 70 (Perry, 2006). Alongside these declines in tactile feedback, proprioceptive feedback is also affected by age, with the sensation of joint position reduced in the lower limbs (Skinner et al., 1984).

These sensory deficits are accompanied by a decline in motor abilities, increasing the risk of falls, impact injuries or inappropriate patterns of muscle contraction. Among contributing intrinsic factors are reduced joint mobility, in part due to mechanical deterioration at the joint surfaces and in muscle, tendon and ligaments. Alongside numerical loss of muscle fibres (Freemont and Hoyland, 2007), muscle strength has been shown to decline by 10-15% each decade after age 30, and as a consequence the resulting risk of falls increases (Paterson et al., 2007). Loss of spinal stability also leads to decreased range of spinal rotation, as observed during standing reach tasks and when twisting when sitting (Cavanaugh et al., 1999, Schenkman et al., 1996).

1.6.2 Balance Control in the Elderly and Infirm

Under normal circumstances, the sub-clinical symptoms of ageing do not affect function as long as the central nervous system can compensate (Woollacott, 1989); Hence, it is not uncommon for the elderly to maintain balance when rotating body segments, and even to perform turning tasks as well as young healthy subjects (Baird and Van Emmerik, 2009, Paquette et al., 2006).

However, this said, it is also known that cognitive demands can have a large impact on older subjects, with even healthy elderly known to have more trouble allocating attention to additional tasks than the young (Shumway-Cook and Woollacott, 2000a, Teasdale and Simoneau, 2001). The prefrontal areas of the brain that are associated with allocation of attention undergo structural change with age (Lezak et al., 1995), and this clearly poses further difficulty to balance control. In dual tasking situations, this often results in one task being performed at the expense of another, for instance talking at the expense of

walking, as performing both simultaneously is challenging (Lundin-Olsson et al., 1997).

The consequences of the increased difficulties in dealing with large sensorimotor load can be observed in the changes in gait patterns used by the elderly during locomotion. For example, some of the reported strategies observed during walking in the elderly include decreases in step length, velocity, and gait speed (Donoghue et al., 2013) and increased variability in the timing of steps (Menz et al., 2003). Generally speaking, a more conservative gait pattern has been described for elderly subjects, and is argued to be even more prevalent when the walking surface is irregular (Menz et al., 2003). This could well be in part due to the decreased somatosensory functions described above.

One of the most common observations when considering the gait of older subjects appears to be the reduction in amplitude and acceleration of independent body segment rotations. The loss of mechanical separation of the head, trunk, and pelvis due to the motor deficits describe above, have been shown to result in reduced independent rotations of the head, shoulders, and pelvis in older subjects (Chiacchiero et al., 2010, Cinelli et al., 2008, Paquette et al., 2006, Van Emmerik et al., 2005). Whilst the increased rigidity and loss of strength in the muscular system clearly plays a large role in this effect, some authors put forward arguments to suggest that reducing and synchronising movement in the upper body segments could also be linked to deliberate strategy. For instance, Van Emmerik et al., (2005) suggest that minimising counter-rotations in the upper body may be employed to increase energy in the trunk in order to compensate for deficits in lower body strength, in particular ankle power. Alternatively, Menz et al. (2003) suggest that by employing reduced gait speed, the elderly are adapting their gait patterns to actively reduce magnitude of head and pelvis accelerations to what they describe as a ’tolerable level’. They go on to stress that the cautious characteristics they observed of the elderly gait are likely linked to reluctance and fear rather than true inability.

In the unhealthy elderly, these effects of normal aging can be further exacerbated. For example, visual deficits known to be prevalent in Parkinson's disease include impaired visual acuity (Jones et al., 1992), contrast sensitivity (Langheinrich et al., 2000, Harris et al., 1992, Regan and Neima, 1984), and colour vision (Pieri et al., 2000, Price et al., 1992). In addition, visual attention and motion perception are also affected (Uc et al., 2005). During locomotion, these deficits manifest as an inability to maintain a straight trajectory, perceive obstacles and doorways, and negotiate uneven terrain, which in turn may lead to gait disturbance through festination, freezing and falls (Nutt et al., 2011).

It has long been known that the coordination of multiple motor components poses a challenge in Parkinson's disease (Benecke et al., 1986). This is particularly prevalent in situations that involve coordinating separate motor tasks, for instance the transition between standing and initiating gait in a sit-to-walk task (Buckley et al., 2008). Typically, the head and trunk move *en bloc* (Vaugoyeau et al., 2006), and pelvic rotation has been found to be limited (Vallabhajosula et al., 2013), possibly indicating loss of ability to uncouple shoulder and pelvic segments to produce effective trunk rotations. Axial rotations are also smaller and slower compared to healthy older adults (Vallabhajosula et al., 2013).

It is important to note however, that there is growing evidence to suggest that the environment can play a large role in the extent to which function in the elderly is affected. Most research into the effects of the built environment on lifestyle are focused on younger and middle-aged adults, whereas sensory deficits associated with older age would clearly suggest that environmental factors would have more of an impact on the elderly and infirm (Sallis and Kerr, 2006). Studies have noted that several factors impact upon the decision of elderly people to take exercise outside, including those with large sensory demands such as traffic and perceived fall hazards (Aronson and Oman, 2004). However, the benefits of physical activity are clear, even improving cognitive function amongst older adults (Angevaren et al., 2008). Crucially, those who

walk outside more often have been shown to be less functionally impaired (Kono et al., 2004), and hence it appears that increasing exposure to environmental situations can to some extent prevent some of the functional decline observed with ageing. These findings have clear implications for the design of urban environments, in order that they might optimise such benefits.

1.7 Postural Control and Human Evolution

1.7.1 The First Habitual Bipeds

It is clear that the control of balance and postural control in modern humans is highly complex, requiring a wide range of motor and sensory capabilities as well as large attentional resources to cope with the considerable cognitive demands. So when did the required motor and sensory skills appear within our evolutionary history?

It can be argued that the first evidence for the adoption of habitual bipedalism (i.e. where bipedal locomotion is the most common locomotor mode) can be associated with the genus *Australopithecus.* Perhaps the most well-known and most debated evidence for habitual bipedalism in archaic human ancestors comes from fossil evidence attributed to *Australopithecus afarensis.* Dated between 2.9 and 3.8 Ma (Johanson and White, 1979), the fossil record for the species is rich, and includes the famous partial skeleton AL 228-1, 'Lucy'. However despite the abundance of postcranial remains, there is considerable debate as to the exact locomotor repertoire of *Australopithecus afarensis.* Some suggest that the significant number of primitive postcranial traits imply that the preferred locomotor mode of the species would have been kinematically different from our own (Stern Jr, 2000, Clarke and Tobias, 1995, Berge, 1994, Duncan et al., 1994, Susman et al., 1984, Stern Jr and Susman, 1983), whereas others argue that the derived adaptations for terrestrial bipedalism enabled the species to walk with a fully erect gait much more equivalent to that of modern humans (Crompton et al., 1998, Latimer, 1991, Latimer and Lovejoy, 1989, Lovejoy, 1988, Latimer et al., 1987, Latimer, 1983). More recently however,

advances in inverse dynamics and evolutionary robotics have now demonstrated that *Australopithecus afarensis* (as represented by 'Lucy') was not only compatible with fully erect bipedalism (Crompton et al., 1998), but that it would in fact have been energetically optimal, with the bent hip bent knee locomotion proposed by Stern and Susman (1983) subject to almost double the energetic cost (Sellers et al., 2005).

The AL-288-1 skeleton demonstrates several postcranial features suggesting significant adaptation to bipedalism. In the femur, this includes a high bicondylar angle implying that the leg would have been positioned close to the midline as in modern man (Johanson and Taieb, 1976). Further, the pelvis also exhibits features for efficient bipedalism, including short, wide iliac blades (McHenry, 1986, Stern Jr and Susman, 1983) which improve gluteal muscle lever arm and hence help counter the torque of body weight (Lovejoy et al., 1973). Despite this however, the morphological configuration of body segments in early australopiths is likely to have impeded the ability to rotate body segments independently of one another, in particular the head and shoulders, and trunk and pelvis. The ribcage had been thought to imply a funnel-shaped trunk as in chimpanzees (Schmid, 1991), although some suggest *Australopithecus* may have had a tall waist (Haile-Selassie et al., 2010). However, overall it is likely to be much wider than that of *Homo*. This would therefore have prevented the efficient counter rotations of the trunk that are thought to be important in counteracting the destabilising torque brought about during leg swing, perhaps indicating a less efficient mode of bipedal locomotion. Furthermore, it has also been argued that australopiths possessed a more cranially orientated glenoid and extensive muscular connections between the head and neck (Stern Jr and Susman, 1983) leading to elevated ('shrugged') shoulders. This in turn would have restricted the independent counter rotation of the shoulders that reduces axial rotation of the head, and may consequently have precluded efficient gaze control.

However, the morphology of later species of australopiths are argued to be much more derived and closer to that of *Homo* and modern humans. *Australopithecus garhi* for example was first discovered in the Middle Awash and dated to c 2.5 Ma (Asfaw et al., 1999). The BOU-VP-12/1 specimen demonstrates a human like humeral/femoral ratio (Asfaw et al., 1999), and crucially therefore marks the earliest appearance of the elongated femur that characterises *Homo.* When compared to *Australopithecus afarensis* therefore, the elongated femur would have increased step length and reduced inertial resistance to acceleration, making *Australopithecus garhi* a more efficient biped. In saying this, the forearm length was much like that of other australopiths (Asfaw et al., 1999), indicating that upper arm – lower arm proportions had yet to reach *Homo*-like proportions.

Arguably the most interesting evidence regarding the behaviour of *Australopithecus garhi,* however, is that relating to tool-making ability and cognition. For a considerable length of time, many researchers regarded tool-making as an ability associated only with *Homo,* however the discovery of stone tools that correlate temporally and spatially with *Australopithecus garhi* (Semaw, 2000) has prompted serious reconsideration. Furthermore, *Australopithecus garhi* has also been associated with cut marks on bovid bones, indicating the use of stone tools in defleshing bones (De Heinzelin et al., 1999). It therefore seems that as early as 2.5 Ma, hominins were beginning to create and use primitive tools, made even more interesting by the fact that brain size had yet to increase to *Homo*-like proportions.

1.7.2 *Homo* – The Predominant Bipeds

While there is a clear diversity in the locomotor repertoire of the australopiths, there is a universal consensus that later species of *Homo* were much more human-like in their bipedal locomotor behaviours. The emergence of the genus in the period between 2.5 and 1.8 Ma can therefore be considered to be directly associated with the emergence of predominant bipedalism. A more definite move to human-like bipedalism can be found with the emergence of

Homo ergaster at c. 1.8 Ma, which is also associated with a move to more open country and savannah environments (Vrba, 1988). The Nariokotome Boy skeleton (KNM-WT 15000) found in Koobi Fora, Kenya (Brown et al., 1985) is human-like and is shown to have been a long distance striding biped capable of effective load carrying (Wang et al., 2004). It demonstrates all derived postcranial traits traditionally associated with such bipedalism, including short arms and long legs - the length of which are similar to those of modern humans (Ruff and Walker, 1993). Two intermediate pedal phalanges are also shorter and less curved than those of *Australopithecus afarensis* (Latimer et al., 1982, Day and Napier, 1964), which has been thought to suggest a more modern pressure distribution. Further, the narrower pelvis and barrel shaped rib cage (Jellema et al., 1993) indicates a move from the long funnel shaped trunk of australopiths, to a shorter barrel shaped trunk which would have aided balance through a higher position of the centre of gravity.

However, despite this evidence suggests that shoulder-configuration and hence trunk counter-rotations were not fully modern until as recently as 12,000Ka (Larson et al., 2007), potentially indicating that *Homo ergaster* would not have been an effective runner. The increased brain size in KNM-WT 15000 of 880cc (Begun and Walker, 1993) may also indicate that improved bipedal efficiency was intrinsically linked to increasing cognitive ability. Indeed, Dunbar's social brain hypothesis suggests that increased range through more efficient locomotion in turn led to increased number and complexity of social contacts, and hence selected for a larger brain size (Dunbar and Shultz, 2007, Dunbar, 2003, Dunbar, 1998). This is supported by evidence suggesting that the distance over which stone tools, or their raw materials, were carried increased from around 2-10km in the Oldowan (Leakey, 1971, Hay, 1976) to potentially over 100km by 1.5 Ma (Clark, 1980), the latter correlating both temporally and spatially with *Homo ergaster*. Tool transport is therefore suggested as a selective factor for increased ranging and hence the more efficient sort-trunked long-legged morphology seen in KNM-WT 15000 (Wang et al., 2004). Overall, such a combination of highly efficient bipedal locomotion and increasing

cognitive abilities would suggest that *Homo ergaster* was well equipped to actively exploit open grassland environments.

The distances over which early species of *Homo* ranged were yet further increased in *Homo erectus,* with fossil evidence indicating a very rapid dispersal out of Africa between 1.7 and 1.8 Ma (Antón et al., 2002, Gabunia and Vekua, 1995, Wanpo et al., 1995). *Homo erectus* demonstrates unequivocally human-like limb proportions, with femoral length indicating that overall leg length may have been up to 50% larger than in *Australopithecus afarensis* (Aiello and Dean, 1990). Further, the substantially larger articular surfaces of the joints of the hind limb when compared to *Australopithecus* also indicate adaptation to increased loading to impact forces at heel strike (Jungers, 1988). The presence of an elongate narrow waist (Jellema et al., 1993) would also have substantially increased the degree of independent rotation of the trunk from the pelvis in *Homo erectus,* which would have been essential in counteracting the legs during running (Bramble and Lieberman, 2004). The dramatic reduction or absence of the extensive muscular connections between the head and shoulders (Aiello and Dean, 1990) when compared to australopiths would have also aided with balancing the destabilising torques produced by leg swing through counter-rotation of the shoulders and arms, and would have also reduced the axial rotation of the head.

Such significant adaptation to running in particular has led to the description of *Homo erectus* as an endurance runner and persistence hunter (Bramble and Lieberman, 2004, Carrier et al., 1984) with its bipedal performance and energetic efficiency markedly improved from that of australopiths. This is reflected in the much more human-like morphology of the semicircular canals of *Homo erectus,* which imply that the vestibular system was much more sensitive to angular accelerations of the head (Spoor et al., 1994). Consequently, despite restrictions in neck motion, the species was likely to have been much more competent at head and gaze stabilisation during locomotion

when compared to australopiths, likely selected for as a consequence of its highly active lifestyle.

1.8 Summary and Gaps in Knowledge

The above discussion raises some important implications regarding the complex and adaptive nature of sensorimotor integration, and the demand it places on neuroprocessing, particularly from the perspective of healthy ageing and the infirm. It is clear that whilst visual inputs in particular are a crucial component of sensorimotor control, there is nonetheless a delicate balance and weighting of sensory information necessary for such control. This is especially the case in more demanding tasks such as dual tasking scenarios that are typical of everyday life. The emerging evidence for the potential use of feedback as a postural control mechanism may therefore be of particular interest in assisting those who may be particularly affected by complex environments. Although, the balance between the benefits and increased cognitive demands of sensory stimuli during locomotion and dynamic movements are yet to be fully established.

It is also clear from the fossil record that whilst definitive adaptations for terrestrial bipedalism are clear from as early as 4.5 and 3 Ma, there is considerable debate about the exact nature of bipedalism in early hominins such as *Australopithecus afarensis*. The consensus that the species did not have a full waist but was certainly substantially capable of effective bipedal walking, at least over short distances, therefore makes it a crucial species for consideration by a human analogue study of segment coupling, as performed in this project. With the full transition to striding bipedalism complete in *Homo ergaster,* later species of *Homo* were consequently much more human-like in the type of bipedalism they practiced. As seen in *Homo erectus,* such species were likely to have been fully competent runners, enabling their rapid expansion and success. Alongside the growing cognitive and balance control abilities discussed, particular interest was placed on these species when considering the sensorimotor implications of this work.

As humans are habitual bipeds, the sole contact that the human body has with the ground is through the plantar surface of the feet. Despite the clear importance this implies for detailing the interactions at this interface with the overall function of foot during gait, recent advances in foot pressure analysis only serve to emphasise the complexity of the issue. The longstanding method for plantar pressure measurement, ten region subsampling (Rosenbaum and Becker, 1997), involves analysing the foot as a series of defined areas, each of which is then allocated a single pressure value. However, with the recent development of techniques to analyse plantar pressures at a pixel by pixel level (Pataky et al., 2008), it has been shown that such subsampling may actually exaggerate or under-represent statistical differences when comparing pressure values. When also considering the very small numbers of pressure plate records typically used in pressure analysis using ten region subsampling, this would suggest a very poor representation of accurate pressure distributions, particularly when considering recent evidence that natural inter- and intra-subject variation in foot pressure distribution has shown to be high, even overlapping that of other apes (Bates et al., 2013b).

The issue of variability is further complicated when considering the morphology and function of the feet of our ancestors. Fossil evidence of foot bones is sparse, and the locomotor conclusions made from even the most complete specimens are the subject of considerable debate due to their complex mosaic of characteristics for both arboreal and terrestrial locomotion (Kidd, 1999, Wood, 1974, Day and Napier, 1964). There are of course fossilised footprints, including the famous trail at Laetoli (Leakey and Hay, 1979), however much controversy still exists surrounding the extent to which actual pressure distribution is reflected in footprints given the insufficiently understood effects of differences in substrate properties. Indeed, recent evidence demonstrates that in modern humans, the overall depth of footprints has a significant effect on pressure distribution (Bates et al., 2013a).

As a consequence, research continues to attempt to find novel solutions to determine the most likely modes of locomotion in our ancestors, particularly those species that had begun to make the transition from dense forest environments to more open grassland and savannahs. Notably this includes *Australopithecus afarensis*, made famous by the 3.2 Ma 'Lucy' skeleton, which possessed an apparent mosaic of features for both terrestrial bipedalism (Latimer and Lovejoy, 1989, Johanson et al., 1982) and arboreal locomotion (Stern Jr and Susman, 1983, Susman, 1983). Consequently, a number of theories have been put forward regarding the gait of *Australopithecus afarensis* ranging from a chimpanzee-like bent hip bent knee gait (Stern Jr and Susman, 1983, Susman et al., 1984) to fully erect bipedalism much like that that of modern humans (Lovejoy et al., 2002, Crompton et al., 1998, Latimer, 1991). Although computer modelling techniques suggest that the latter is most probable (Crompton et al., 1998), as yet the changes in foot pressure distribution that might have accompanied the transition from arboreal locomotion in dense woodland to habitual bipedalism in open environments are yet to be considered.

Further, despite the known increase in the size of the semicircular canals in *Homo* (Spoor et al., 1994), and hence enhanced abilities for gaze and head stabilisation, the corresponding implications for adaptations in sensory processing that likely contributed to the efficiency of *Homo erectus* as a habitual biped, and its success as an endurance runner (Bramble and Lieberman, 2004) and persistence hunter (Carrier et al., 1984), have also as yet remained unassessed.

1.9 Research Question and Overarching Hypotheses

The literature review above details the existing knowledge regarding the efficiency of modern human sensorimotor and postural control, the wide ranging theories surrounding the gait of ancestral hominins, and how the two are intrinsically linked. In doing so, it not only serves to highlight the gaps in knowledge that are yet to be answered, but also demonstrates that data from

modern human analogues could provide novel insight into specific species of hominin which are surrounded by continuing debate.

As a consequence of the gaps in knowledge identified above, this project aimed to answer the following research question:

'How might increased sensory demand and the recoupling of body segments in modern humans impact on postural control, and what are the implications with respect to the built environment, ageing, and the evolution of human postural control?'

From this research question, two overarching hypotheses were developed:

1) **Sensory prioritisation during walking will result in alterations to postural control as attention is allocated to secondary tasks of varying complexity.**

2) **The recoupling of the head and neck, and trunk and pelvis, will result in alterations to postural control as a consequence of the increased rigidity of the thorax segments.**

1.10 Thesis Outline

In order to test these hypotheses, this thesis has conducted a unique combination of foot pressure, kinematic, and eye movement analysis during walking. As such, it provides a unique contribution to knowledge of the impacts of sensory load and the restriction of body segments on human foot pressure variability. The results of the studies are relevant to both the evolution of bipedalism, and also to modern ageing.

The three study chapters of this thesis, Chapters 3, 4 and 5, were designed and executed with two overarching hypotheses, laid out in Chapter 1.9, in mind.

Chapter 3 presents the results of a study assessing how foot pressure variability was affected by visual object tracking against varying levels of visual clutter. This involved the comparison of foot pressure records made during gaze fixation of a static object with those made during smooth pursuit against backgrounds of varying complexity.

Chapter 4 extends the object tracking task considered in Chapter 3 by incorporating a dual auditory task. This enabled the comparison of the impact of filterable background auditory stimuli with a repeat-back language task requiring an active response, and the potential effects of processing prioritisation on foot pressure variability.

Chapter 5 considered the effects of the restriction of independent counter-rotations of body segments on whole body kinematics and foot pressure variability through the use of medical body braces.

Chapter 6 summarises the results and conclusions made throughout this thesis. The results of the studies are discussed with respect to the hypotheses of their respective studies, and are then discussed together in the context of the overall research questions laid out above. Finally, the wide ranging implications of the results are considered, and limitations and opportunities for further work are discussed.

Chapter 2: Materials and Methods

This thesis set out with two overarching hypotheses in mind: 1) Sensory prioritisation during walking will result in alterations to postural control as attention is allocated to secondary tasks of varying complexity; and 2) The recoupling of the head and neck, and trunk and pelvis, will result in alterations to postural control as a consequence of the increased rigidity of the thorax segments.

In order to address these hypotheses, this thesis consisted of three studies involving the collection and analysis of foot pressure, kinematic, and pupil movement data. Of the three study chapters of this thesis, Chapters 3 and 4 investigate the first hypothesis, and Chapter 5 investigates the second. As the exact methods used for each study conducted as part of this project differ, this chapter presents an overview of the equipment, software, and data processing used. The exact protocols for each study are detailed within their own respective chapters below.

2.1 Equipment

Various pieces of equipment were used in the collection of data for this project. For all studies within this thesis, this included a Zebris FDM-T pressure sensitive treadmill (Isny im Allgäu, Germany) instrumented with an integrated sensor matrix for foot pressure measurement (Figure 2.1). This matrix consists of over 5000 sensors per 150cm x 50cm area, and hence provides a high quality and detailed record of foot pressures during walking. The treadmill was connected to a computer running the associated Zebris software, Win-FDM (Isny im Allgäu, Germany), through which data collection and processing was initiated.

Using Win-FDM, each foot pressure record is captured as a complete footstep from heel strike to toe off. As the system can correct for the effect of the movement of the treadmill belt over the sensors, completely stable foot rollover

patterns are captured. For each foot pressure record, a pressure value (N/cm^2) is recorded for each sensor in contact with the plantar surface of the feet.

Figure 2.1: Zebris-FDM foot pressure sensitive treadmill.

The resulting values for each pressure sensor are then displayed as a colour map image in order to represent diagrammatically the relative pressure distribution under the different areas of the foot. In each image, the largest pressure values are displayed as ‘hot’ colours, and the lowest pressure values are displayed as ‘cool’ colours (Figure 2.2). The treadmill was run at a frequency of 100Hz, and typically, for a subject walking at a slow, consistent speed of 1.1 m/s^{-1}, around 200 foot pressure records were collected in a 2 minute trial, producing large sample sizes in a short period of time.

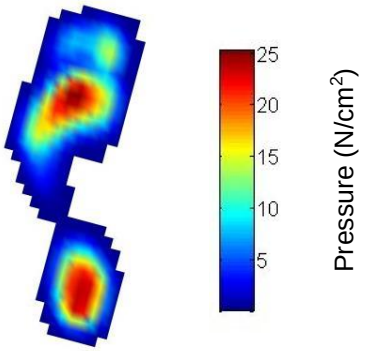

Figure 2.2: Exemplar foot pressure record displayed as a colour map. Colour bar represents actual pressure (N/cm^2).

When collecting kinematic data alongside foot pressure data to study the second hypothesis (specifically for Chapter 5), the trigger-out capability of the pressure sensitive treadmill enabled the automatic triggering of a 9-unit Qualisys ProReflex (Gothenberg, Sweden) motion capture camera system when foot pressure recording was initiated. This therefore allowed for accurate synchronisation when capturing foot pressure and kinematic data. In order to collect accurate 3D kinematic data, the motion capture camera system must first be calibrated. Using the Qualisys Track Manager (QTM) software (Gothenberg, Sweden), an X,Y,Z coordinate system is defined using a stationary calibration frame, over which a calibration wand is moved to define the volume of the experimental area and hence calibrate the system (Figure 2.3). When a series of Qualisys 19mm retro-reflective markers (Gothenberg, Sweden) are then attached to anatomical landmarks on the body of a subject, they reflect back the infra-red light emitted by the cameras (Figure 2.4). As the cameras detect these reflections, the system is then able to calculate the global coordinates of each marker at a frequency of 100Hz (matching that of the treadmill), providing an accurate record of the movement of body segments of interest.

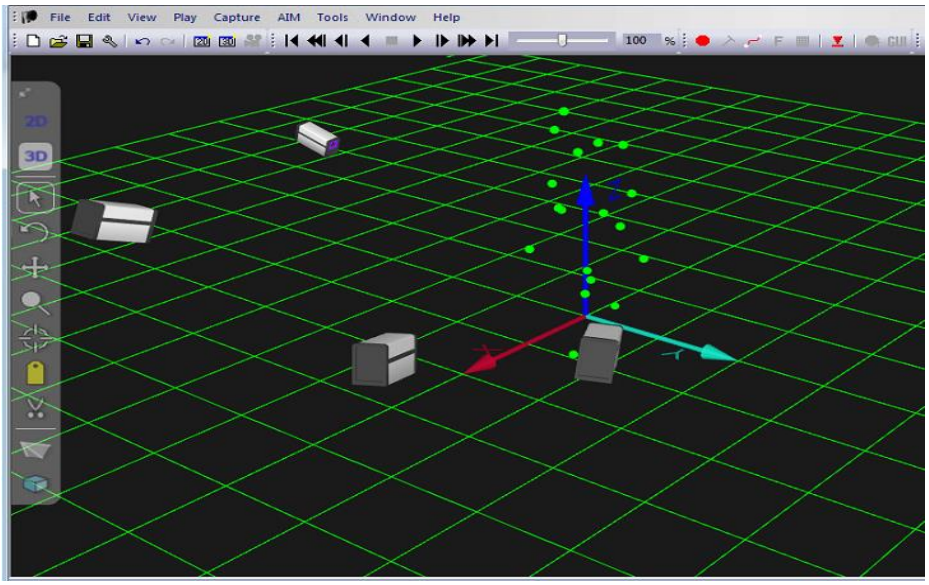

Figure 2.3: Example of the X,Y,Z coordinate system as seen in QTM. During processing, QTM shows the relative position of the motion capture cameras to the subject, a few of which are seen from this angle. Each green dot represents a reflective marker positioned on an anatomical landmark on the subject.

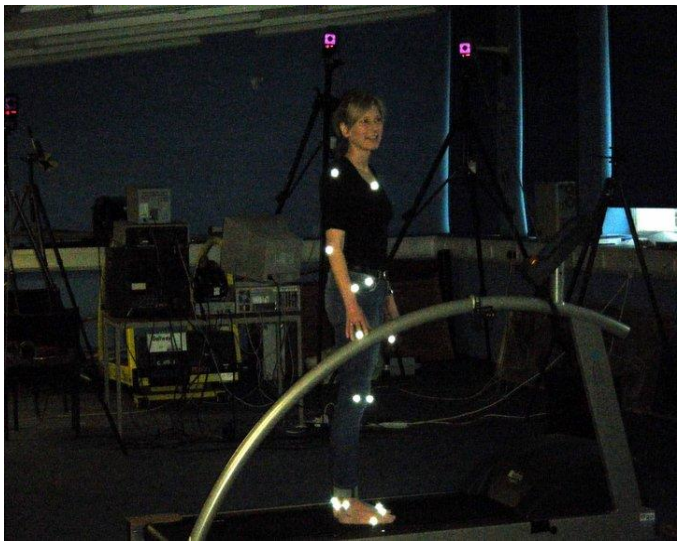

Figure 2.4: Infrared light emitted by the motion capture cameras is reflected back from retro-reflective markers attached to anatomical landmarks on the subject. The global coordinates for each marker are then tracked.

For studies investigating the first hypothesis in which subjects were required to track a visual object (Chapters 3 and 4), an eyetracker was used to

measure pupil movement. Two different models of eyetracker were used in this project.

The first was a monocular eye-tracking system, the Eye-trac 5000, Applied Science Laboratories (ASL) (Bedford, MA, USA), mounted on a Bauer HH1000L Ice Hockey helmet (Exeter, NH, USA). This system tracks eye movement using similar principles to that of the motion capture camera system. An infrared video camera is directed at the pupil, the light from which is reflected off the corneal surface (known as the specular reflection) and is detected by the camera.

The second was a binocular eye-tracking system, the ViewPoint BSU07 USB-60x3, Arrington Research (Scottsdale, AZ, USA), mounted on a goggle-based system. In this case, the system uses a 'dark pupil' approach in which the video cameras directed at the eyes are able to distinguish the pupils based on colour depth. Once defined the cameras then track the movement of the entire pupil. Despite differences in the methods of tracking between the systems, both provide the XY coordinates of the pupil(s) throughout a trial. Both therefore generate an accurate representation of pupil movement in both the horizontal and vertical planes.

2.2 Data Processing

2.2.1 Pupil Movement

For the two studies (Chapters 3 and 4) in which pupil movement data was collected, the eye tracking profiles for each trial were used solely to confirm that efficient object tracking had taken place. As this project involved subjects alternating between periods of gaze fixation and smooth pursuit whilst walking on the treadmill, it also enabled the definition of each separate instance of each of these tracking types. The decision not to further analyse pupil movement data was taken due to the length of time required to prepare and analyse foot

pressure data, the primary dependent variable for all experiments conducted within this thesis (see chapter 2.2.2 for description).

In order to utilise the pupil movement data for a trial, it was first exported in TSV format into MATLAB. Because of the differences in the format of the data files generated by the two eyetrackers, two slightly different versions of code were written to read in pupil movement data and to identify the timings for each period of each gaze tracking type. For the monocular Eye-Trac system, horizontal pupil positon was read in from the TSV file and a figure generated with horizontal pupil position at each frame of capture plotted as a line graph (Appendix A1.1). Using a series of crosshairs, each exact transitional point on this graph was marked to identify the points at which the subject switched between gaze fixation and smooth pursuit and vice versa (Figure 2.5). The frame numbers for each selected point were then returned and could then be manually converted to a value in seconds. For example, if the first exact period of gaze fixation occurred between frames 1 and 1200 frames, this was equivalent to the first 20 seconds of the trial (1200 frames / 60Hz = 20 seconds). The timings in seconds were then stored in a variable named ‘CutPoints’.

For the ViewPoint code, pupil position data for both eyes was read in from the TSV file (Appendix A1.2), and a figure generated on to which the line graphs of horizontal pupil movement of both eyes were superimposed. This ensured that the data for both eyes was synchronous, and hence that data acquisition was effective. If this was not the case then the trial was repeated. As with the code for Eye-Trac data, the exact transition points between tracking points were identified by marking crosshairs on the figure (Appendix A1.3) (Figure 2.6), however in this instance the ‘CutPoints’ file containing the timing information in seconds was generated automatically within the code.

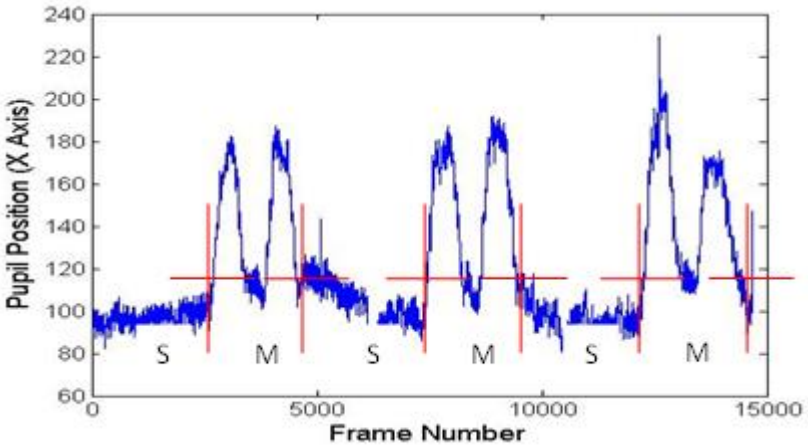

Figure 2.5: Exemplar eye tracking profile of horizontal pupil movement measured using the Eye-Trac system. Red crosshairs mark the transitions between the gaze tracking types. Segments marked 'S' indicate the portions of the trial where the target is stationary and gaze fixated. Segments marked 'M' indicate areas of target movement, and hence smooth pursuit occurrence.

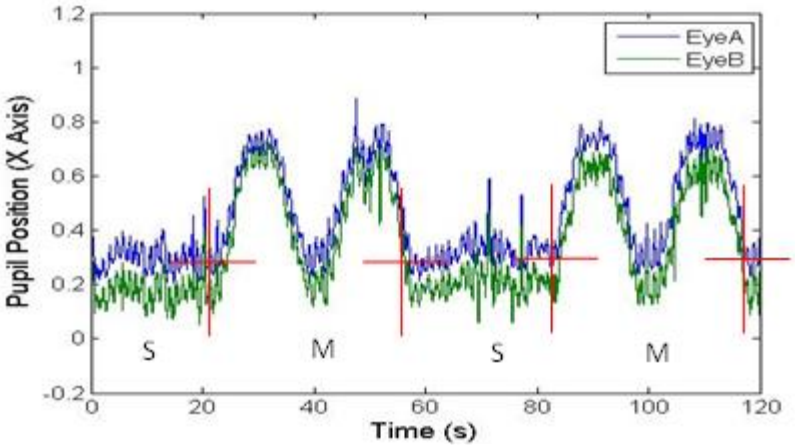

Figure 2.6: Exemplar eye tracking profile of horizontal pupil movement measured using the ViewPoint system. Red crosshairs mark the transitions between the gaze tracking types. Segments marked 'S' indicate the portions of the trial where the target is stationary and gaze fixated. Segments marked 'M' indicate areas of target movement, and hence smooth pursuit occurrence.

2.2.2 Foot Pressure Records

Firstly, the treadmill output for each trial was exported in ASCII format from the Win-FDM software that runs data acquisition for the Zebris treadmill. The peak pressure record for each footprint made during the trial was read into MATLAB and stored as a numerical series of pressure records using in-house

code (Appendix A1.4). This outputted and stored information regarding the numbers of left and right foot records and the sampling rate in a file named ‘proc_info.m’

The CutPoints variables containing the timing information for the periods of tracking type during each trial, and their corresponding treadmill ‘proc_info’ outputs, were then used to identify which foot pressure records in each trial were made during each period (Appendix A1.5). A ‘buffer’ of one second was applied either side of each of the exact transitional timings defined in the CutPoints variable in order to be confident that no foot pressure records were included in subsequent analysis that may have been made across both tracking types. In each instance, a foot pressure record was only included within a group if it was made wholly within the exact timings specified for that group. This then identified the sequence numbers of the left and right foot records belonging to each time period (for example, the first period of gaze fixation may have contained left foot record numbers 1-36 and right foot record numbers 1-37)

Once the foot pressure records in each trial had been allocated to each defined time period in this manner, a group of records could then be built for each period of gaze fixation and smooth pursuit in the trial. Further in-house code (Appendix A1.6) returned an array of records for each group. It also resized the records to a standard number of pixels, and re-orientated all right foot records to left foot orientation, in order that they could be registered to one another. Finally, all groups of foot pressure records made during gaze fixation were combined, and all those made during smooth pursuit combined, to produce a single array of foot pressure records made during each tracking type. The foot pressure records were then ready for statistical analysis.

In order to then compare foot pressure records statistically, the data were processed in MATLAB using an in-house toolkit, pedobarographic Statistical Parametric Mapping (pSPM) (Pataky and Goulermas, 2008). pSPM involves the use of a series of automated processing steps developed from techniques used to process functional MRI (fMRI) images (Friston, 1997) which enable the

analysis of brain imaging data sequences. By optimising the overlap of homologous structures between all foot pressure records in an array, pSPM enables statistical comparison at a pixel by pixel level, thereby removing the possibility of the over-exaggeration or under-representation of plantar pressure levels that may result from the traditional 10 region sub-sampling approach (Pataky and Goulermas, 2008). Conducting pSPM on an array of foot pressure records involves a series of processing steps as described below:

Firstly, the foot pressure records were registered to one another using the within subject registration option of our in-house pSPM processing toolkit (Appendix A1.7), as all records in each array were made by the same subject. It is during this registration that the records were transformed to overlap optimally by translating and rotating each foot pressure record around its centroid (Pataky and Goulermas, 2008). This therefore took into account the slight differences in the orientation of each record resulting from natural differences in foot placement (Figure 2.7). To conduct this transformation, the first record in the data set acted as a template to which the rest of the prints were aligned. To avoid any bias resulting from registering the records to a single print, the mean peak pressure record from this registration was then calculated and a second registration is conducted using this mean as the template.

However, the calculation of a mean peak pressure record from a large number of foot pressure records, with considerable natural variation in their shape, can result in extraneous ‘noise’ around the periphery of the print of no pressure value. The final processing step is therefore a thresholding step. To remove such extraneous data, and prevent it from impacting upon the results of statistical tests, the foot pressure records were thresholded (Appendix A1.8). The mean of the thresholded records was then calculated, and was itself also thresholded. Finally, the thresholded records were registered to the thresholded mean (using the same registration method as above). All foot pressure records in the array were then directly comparable at a pixel by pixel level.

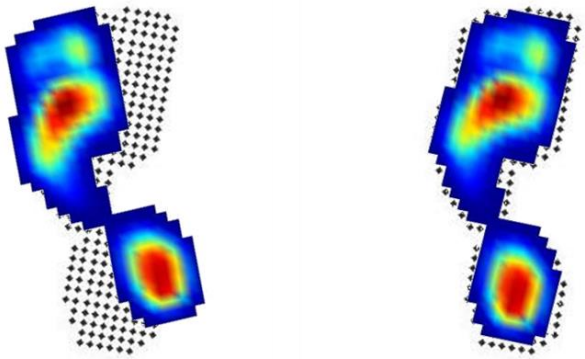

Figure 2.7: Registration of foot pressure records transforms each record to align with a template print. Pressure records are rotated around the centroid to optimally overlap the template image (represented here as a dot-based image).

After completing this pSPM processing, the foot pressure records can be statistically compared. In this project, mean square error (MSE) analysis was conducted in MATLAB in order to provide a quantitative measure of variability of each foot pressure record in a set from the mean peak pressure distribution. The advantage of such methods is that by returning the MSE for each foot pressure record, the resulting value takes into account the differences in pressure at each individual pixel, whereas simply calculating a mean pressure value across all pixels in the record would average out any variation across the record. Variance in MSE was then calculated for each group of records in order to provide a quantitative representation of variability in foot pressures within a group. Multivariate repeated measures Analyses of Variance (ANOVA) were then conducted in SPSS (Chicago, IL : SPSS Inc) in order to statistically compare the variance in foot pressure mean square error in different sensory environments.

2.2.3 Kinematics

Initial processing of kinematic data was conducted in Qualisys Track Manager (QTM). For each motion capture trial, each measured anatomical

landmark was identified and labelled through its corresponding reflective marker. Once all markers had been labelled, the quality of the tracking of each was assessed. If a landmark was tracked for less than 80% of the total trial the results for that segment were considered unrepresentative and discounted. The global coordinates for each of the landmarks were then exported as a TSV file for analysis in MATLAB.

Using an in-house kinematic processing toolkit 'QTrackTools', the marker numbers and coordinate data were identified and placed into arrays (Appendices A1.9 and A1.10). These arrays contained the XYZ positions of each marker at each frame of capture. Using this global information, the angle between two markers in a plane of interest could be calculated at each frame of capture and the list of values returned in an array (Figure 2.8) (Appendix A1.11), hence identifying the range of motion of the associated body segment at each frame. If the minimum and maximum angles are then identified, a maximum range of excursion (in degrees) for the segment can be calculated. These maximum excursion values are calculated for each body segment of interest in each trial, and an overall mean maximum range of excursion and standard deviation is then calculated. Statistical comparisons were made using repeated measures ANOVAs in SPSS.

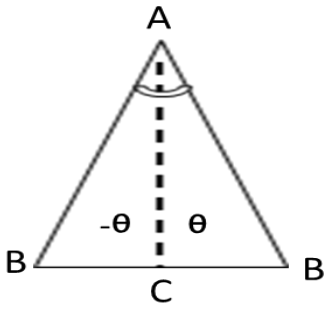

Figure 2.8: Angles (θ) calculated were those between two anatomical landmarks A and B. The angle measured is based on the intersection of vector A-B with the axis of interest (defined by A-C) hence the position of the distal trajectory B relative to that axis determined whether the angle was positive or negative.

2.3 Ethical Considerations

Ethical permission for all experiments was granted by the University of Liverpool Research Ethics Committee (RETH000888). All subjects were provided with information sheets (Appendix A1.12) and gave informed prior consent (Appendix A1.13). Subjects were advised that they could withdraw at any time. In line with University of Liverpool Data Storage and Protection policy, all data was stored securely and anonymously.

Chapter 3: The Impact of Gaze Control During Walking

3.1 Introduction

As primates, modern humans are one of few species to have acquired the ability to centralise moving images on the fovea, the region of the retina where visual acuity is greatest, and track them with clarity using smooth pursuit eye movements (Collewijn and Tamminga, 1984). By minimising the movement of the image on the retina (Carpenter, 1988), smooth pursuit eye movements ensure that the image is maintained on this receptor-dense region; hence, the individual can attend to objects of interest appropriately.

Smooth pursuit is just one of the processes contributing to gaze control, a behaviour composed of a combination of eye and head movements, that acts alongside inertia of the head (Peng et al., 1996, Keshner and Peterson, 1995) to maintain stable vision. This includes the less complex optokinetic reflex and saccadic eye movements, which contribute to gaze fixation on a static target (Walls, 1962, Westheimer, 1954, Dodge, 1903). This visual input is then integrated with those of the vestibular and somatosensory systems in order to derive estimates of self-motion and position which are fundamental to balance. In turn, the vestibulo-spinal reflex is then able to co-ordinate movements of the head and neck with the trunk and ankles (Carpenter et al., 2001, Allum and Pfaltz, 1985).

Despite a need for information regarding the position of the body in space, more complex visual inputs may actually have a detrimental effect on balance. For instance it has been known for some time that smooth pursuit eye movements cause increased levels of postural sway when compared to saccadic eye movements (Straube et al., 1989). This effect is thought to be a consequence of the multisensory reweighting that prioritises (up-weights) or de-emphasizes (down-weights) a sensory input based on the most immediate need (Schweigart et al., 2003); for example, posture appears to acquiesce to the active role of vision in certain situations (Logan et al., 2010). Indeed, Logan

et al. noted that the gain of the hip and shoulder relative to visual scene motion during walking was significantly larger when compared to standing posture. The authors attribute this to differences in the role of vision between the static and dynamic postures, suggesting that the role of vision in providing estimates of self-motion during standing is expanded to that of predictive navigation and obstacle avoidance during walking. As such, they argue that the increased gain may actually reflect reduced resistance to perturbation (i.e. an active switch to a less stable state) in the anterior-posterior plane to enable stepping and better navigation through the environment.

The mechanisms integrating this sensory feedback in order to produce co-ordinated movements during locomotion are increasingly well understood in terms of standing posture (Maylor et al., 2001, Shumway-Cook and Woollacott, 2000a, Shumway-Cook et al., 1997, Maylor and Wing, 1996, Day et al., 1993); however the potential effects on these processes during dynamic movements and locomotion have received much less attention. This imbalance is striking given the importance of factors such as navigation and obstacle avoidance, as well as of the input of other stimuli and other cognitive processes, for example processing and responding to auditory stimuli (Imai et al., 2001, Moore et al., 1999, Paige, 1994a, Bloomberg et al., 1992), which may further up-weight the importance of vision when compared to standing posture.

The effects that visual prioritization might have on postural stability during dynamic movements are therefore yet to be fully established. This study assesses how smooth pursuit eye movements made against backgrounds of varying levels of visual clutter impact on foot pressures and stability during locomotion in young, healthy subjects. Participation was limited to such subjects due to the potentially confounding factors of the visual and motor decline associated with ageing. It was predicted that since postural stability adjusts to support object tracking, the particularly important role of smooth pursuit in tracking moving targets would lead to larger variation in foot pressures when compared to gaze fixation on a static target, for which demand on processing is

lower (Hypothesis 1). It was also predicted that increasing levels of visual clutter during tracking would lead to a further increase in variation in foot pressures (Hypothesis 2), as resolving the target object amongst the background becomes more difficult.

3.2 Methods

3.2.1 Subjects

Ten healthy subjects participated in this study. In order to be included, participants had to be clear of known neurological, vestibular deficits, diabetes, and musculoskeletal pain, amongst other limitations. All subjects had normal or corrected-to-normal vision. Subjects gave informed prior consent, and ethics approval was obtained from the University of Liverpool Research Ethics Committee (RETH000888).

3.2.2 Experimental Setup

Foot pressure data were collected from a Zebris FDM-THM foot pressure sensing Treadmill (Isny im Allgäu, Germany) at a frequency of 100 Hz. Pupil movement data was synchronously captured using a monocular eye-tracking system, Eye-trac 5000, Applied Science Laboratories (ASL) (Bedford, MA, USA) sampling at 60Hz. The system was mounted on a Bauer HH1000L Ice Hockey helmet (Exeter, NH, USA) that was fit-adjustable, so that it was possible to prevent movement of the eye tracker system relative to the head. An LCD projector (NEC NP2250) was used to project visual targets on to a curved projection screen (Beamax A-Velvet, 282 x 166cm) positioned 2m directly in front of the treadmill so as to block and peripheral visual information and distractions. An example set up can be seen in Figure 3.1.

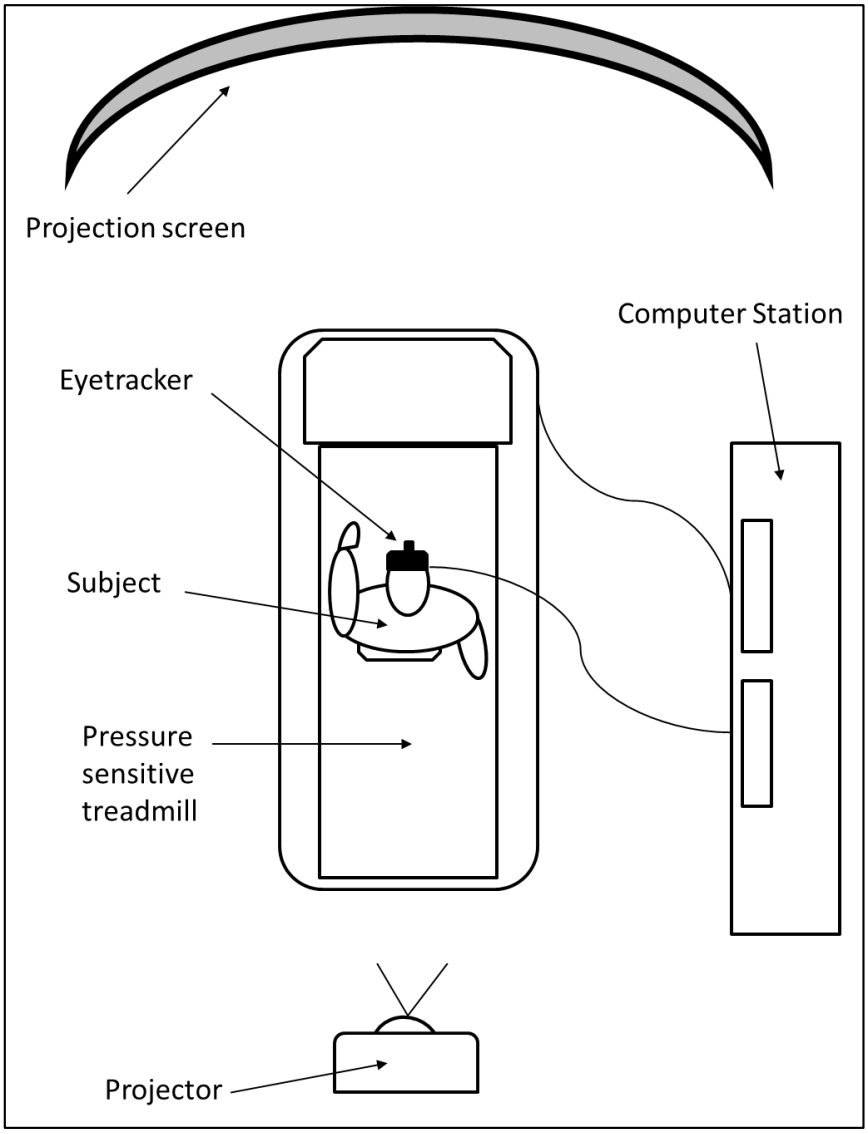

Figure 3.1: Diagrammatic representation of the experimental set up, including the eyetracker, pressure sensitive treadmill, projector, and curved projection screen.

3.2.3 Protocol

Subjects walked on the pressure sensitive treadmill at a set speed of 1.1 m/s^{-1} whilst tracking the movement of a dot-shaped visual target projected on to the screen. This speed was chosen as all subjects confirmed that they felt secure walking at this speed, and since all were able to track the target efficiently (as demonstrated by their eye tracker profiles, see below). This speed

is also comparable with those of natural walking, with an observed range of self-selected speeds of young adults of 0.71-1.76 m/s^{-1} (42.76 - 105.57 m/m^{-1}) (Waters et al., 1988). The visual target alternated between stationary phases and periods of movement in order to initiate periods of gaze fixation and smooth pursuit respectively. The sequence lasted for four minutes, and included three stationary phases of 40 seconds, and three movements of 40 seconds. In each period of movement, the target moved horizontally and in both directions (left-to-right, and right-to-left), however for each of the three periods the vertical path of the target varied in order to prevent learning and associated anticipatory smooth pursuit eye movements. The subjects were made aware of the fact that the target would cycle between stationary pauses and movements, but the only instructions given were to track the object at all times, while walking and moving as freely as they would normally, within the constraints of the treadmill environment. This task was repeated against three different static backgrounds: a blank background (except for a central crosshair focal point), a savannah scene, and a forest scene, to represent the effects of increasing background visual clutter during smooth pursuit. The level of clutter in each scene was assessed quantitatively using MATLAB code designed by Rosenholtz et al. (2007) in order to confirm that the levels of visual clutter in each scene were quantitatively different (Figure 3.2). Visual clutter levels were determined using the feature congestion principle which computes clutter ‘maps’ representing the colour, texture, and orientation of features in an image, before combining and scaling these to provide an overall clutter value.

Figure 3.2: Background images representing each of the three visual clutter levels tested. Values represent feature congestion scalar values generated using the feature congestion code of Rosenholtz et al. 2007.

During each trial, the experimental area was kept clear of any non-experimental visual and auditory stimuli so as not to distract the subject from the task. This included mandating the absence of any staff or subjects not involved in data collection from the experimental area, and the prevention of any staff movement or communication within the experimental area. Further, a 'warning light' outside the lab was in use throughout each trial to prevent anyone from entering or disturbing the laboratory whilst the trials were in progress.

3.2.4 Data Analysis

Pupil movement data captured by the eye tracker was imported into MATLAB (MathWorks, USA) , and for each trial the movement of the pupil in the X (horizontal) plane was plotted as a line graph, enabling the different phases of the trial to be clearly segmented (Figure 3.3).

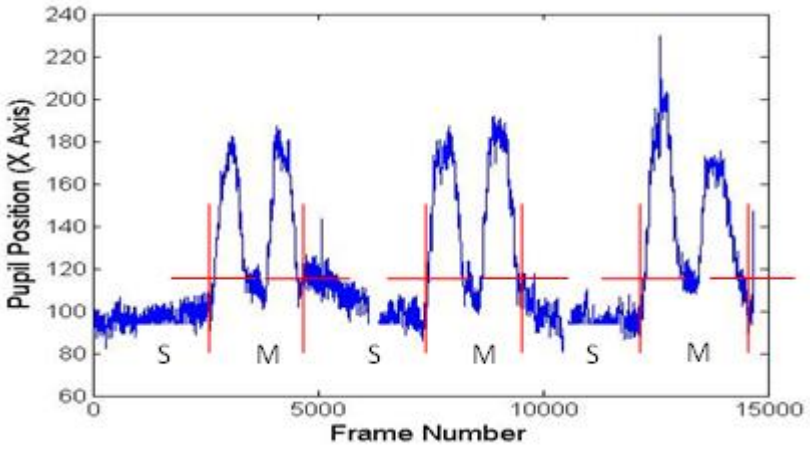

Figure 3.3: Exemplar eye tracking profile of horizontal pupil movement. Red crosshairs mark the transitions between the gaze tracking types, buffers around which allowed the removal of pressure records made during transitional phases from the data set. Segments marked 'S' indicate the portions of the trial where the target is stationary and gaze fixated. Segments marked 'M' indicate areas of target movement, and hence smooth pursuit occurrence.

Using in-house MATLAB code (Appendix A1.1) the start and end points of each phase were marked by drawing cross hairs on the line graph (Figure 3.3) for each trial, and the corresponding frame numbers were recorded. A one second buffer was added either side of each crosshair to avoid analysing any foot pressure records from transitional periods. The timing information was then matched with the frame numbers and timing data generated by the pressure sensing treadmill, and used to separate the foot pressure records into those made during gaze fixation and those during smooth pursuit (Appendices A1.4 – A1.6). For any trials in which the eye tracking profile was unsatisfactory, for instance where the pupil movement was particularly erratic and noisy, or it was clear that it had not tracked the target in the X plane, the data were discounted and the trial repeated (see Appendices A2.1 - A2.10 for the eye tracking profiles of each subject).

The foot pressure groups thus formed were then analysed using in-house software package, pedobarographic Statistical Parametric Mapping (pSPM) (Pataky et al., 2008) (Appendices A1.7 and A1.8). The parametric mapping

technique was originally developed (Friston, 1997) as a series of algorithms for use with images produced during functional magnetic resonance imaging (fMRI) scans. pSPM registers each foot pressure record to all others in the data set so that smoothly varying pixel fields optimally overlap. This then enables comparisons to be made between the foot pressure records at the pixel level. The pressures in each record are represented using a false colour scale, where the hotter colours show areas of highest pressure.

3.2.5 Repeatability

As only one trial was conducted for each combination of visual scene and visual tracking type, repeatability testing was conducted to ensure that the foot pressure patterns were representative and repeatable. A subject was chosen at random to undergo this testing (subject 9), and after initial collection of the first data set, the subject repeated each of the trials 5 times. With both tracking types and all three clutter levels tested on each repeat, this resulted in 30 foot pressure record sets. The repeats were spread over the space of a month to ensure no bias was introduced from fatigue or learning.

3.2.6 Statistical Analysis

Once groups of foot pressure records had been prepared using pSPM, the mean square error was calculated for each foot pressure record within each group in order to define quantitatively how each record differed from the mean (see Appendices A2.11-A2.20 for diagrammatic representations of mean square error variance for each subject). The variance in mean square error for each group was then calculated and used as a measure of overall variability in foot pressures within the group. All subsequent statistical analysis was performed in SPSS (IBM, UK). A repeated measures ANOVA following Bonferroni correction was used to compare overall variance in foot pressure mean square error within subjects across both types of visual tracking (gaze fixation and smooth pursuit), and all three visual clutter levels (blank, savannah, and forest scenes). For the repeatability testing, a repeated measures ANOVA was used to compare variance in foot pressure mean square error within each of the six visual

tracking and visual clutter level combinations (gaze fixation with blank, savannah, and forest scenes; and smooth pursuit with blank, savannah, and forest scenes) across each repeat.

3.3 Results

3.3.1 Foot Pressure Variability

A repeated measures ANOVA was used to determine the effects of visual tracking type and visual clutter level on foot pressure variability. Results demonstrated significant overall between-subject variability in foot pressure mean square error (F (1, 9) = 21.32, p = 0.001), indicating that foot pressure variability was highly variable across subjects. Within-subject results demonstrated only minor within-subject differences in variance in foot pressure mean square error between the visual tracking types (gaze fixation = 6.95 ± 1.47 and smooth pursuit = 6.20 ± 1.41), and indeed these were found to be insignificant (F (1, 9) = 2.72, p = 0.13) (Figure 3.4).

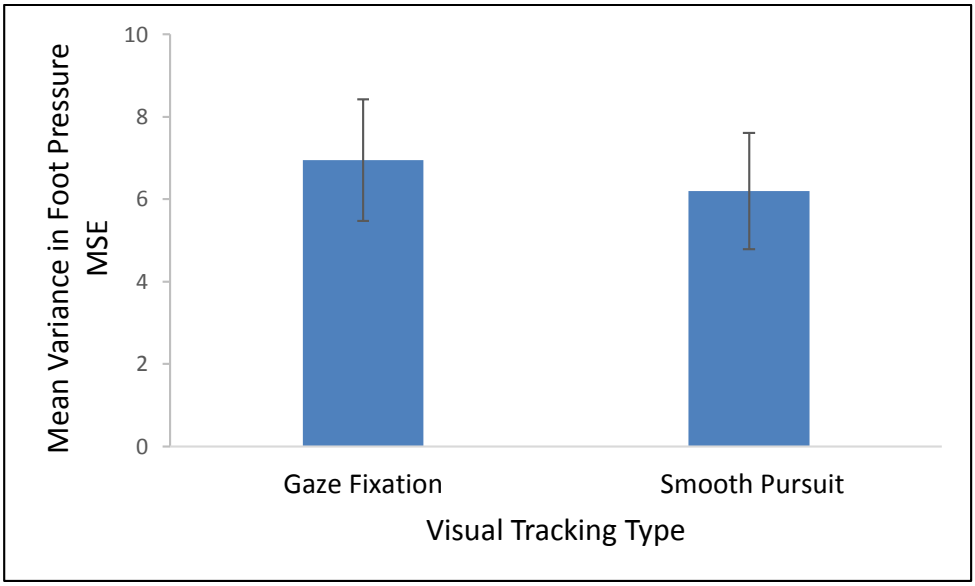

Figure 3.4: Comparison of variance in foot pressure mean square error (MSE) during object tracking using gaze fixation and smooth pursuit.

However, larger within-subject differences in variance in foot pressure mean square error were seen during tracking against the blank, savannah, and forest visual scenes (8.24 ± 1.27, 5.57 ± 1.15, and 5.91 ± 1.35 respectively), and the effect of visual clutter was found to be significant (F (2, 18) = 7.33, p = 0.005). Post-hoc pairwise comparisons following Bonferroni correction determined that the variance in foot pressure mean square error during tracking against the blank visual scene was significantly higher than when tracking against the forest scene (p = 0.04) (Figure 3.5). The effect of the interaction of visual tracking type and visual clutter level on variance in foot pressure mean square error was insignificant (F (2, 18) = 2.28, p = 0.57).

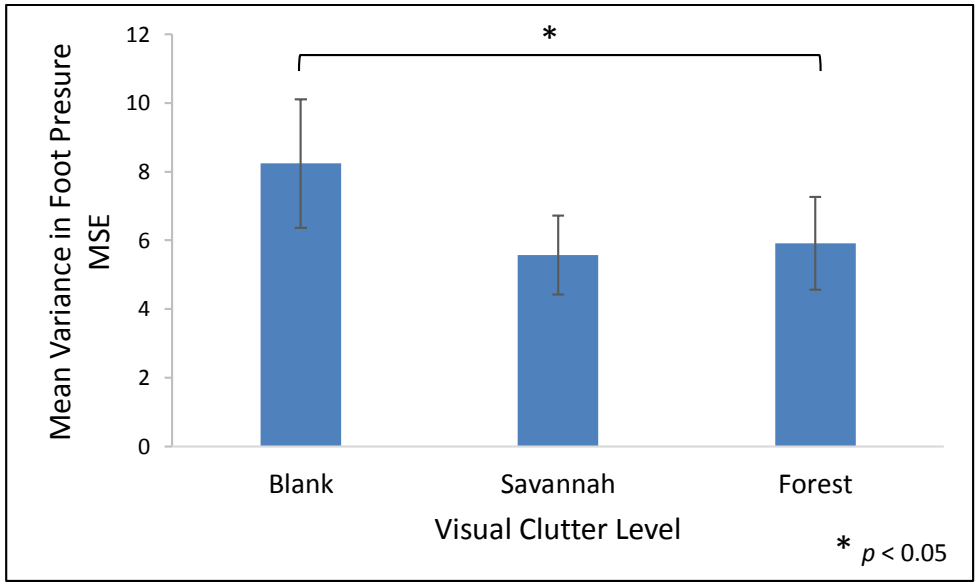

Figure 3.5: Comparison of variance in foot pressure mean square error (MSE) during object tracking across three levels of background visual clutter.

Following this significant difference in variance in foot pressure mean square error across visual clutter levels, and to assess further how foot pressures varied when tracking against the different clutter levels, a visual comparison of the mean foot pressure record to the most varied foot pressure record (that with the highest mean square error) across the levels provides a qualitative impression of how foot pressure might vary with each condition

(Figure 3.6). Figure 3.6 indicates that under-heel pressure remains relatively constant, and that differences expressed in the most variable prints are under the forefoot. These differences in underfoot pressure range through a more diffuse pressure across the lateral forefoot and midfoot (seen e.g. in subjects 1, 3 and 4), and a shift in pressure under the medial forefoot and hallux (seen e.g. in subject 10) to a combination of both (subjects 2 and 5-9).

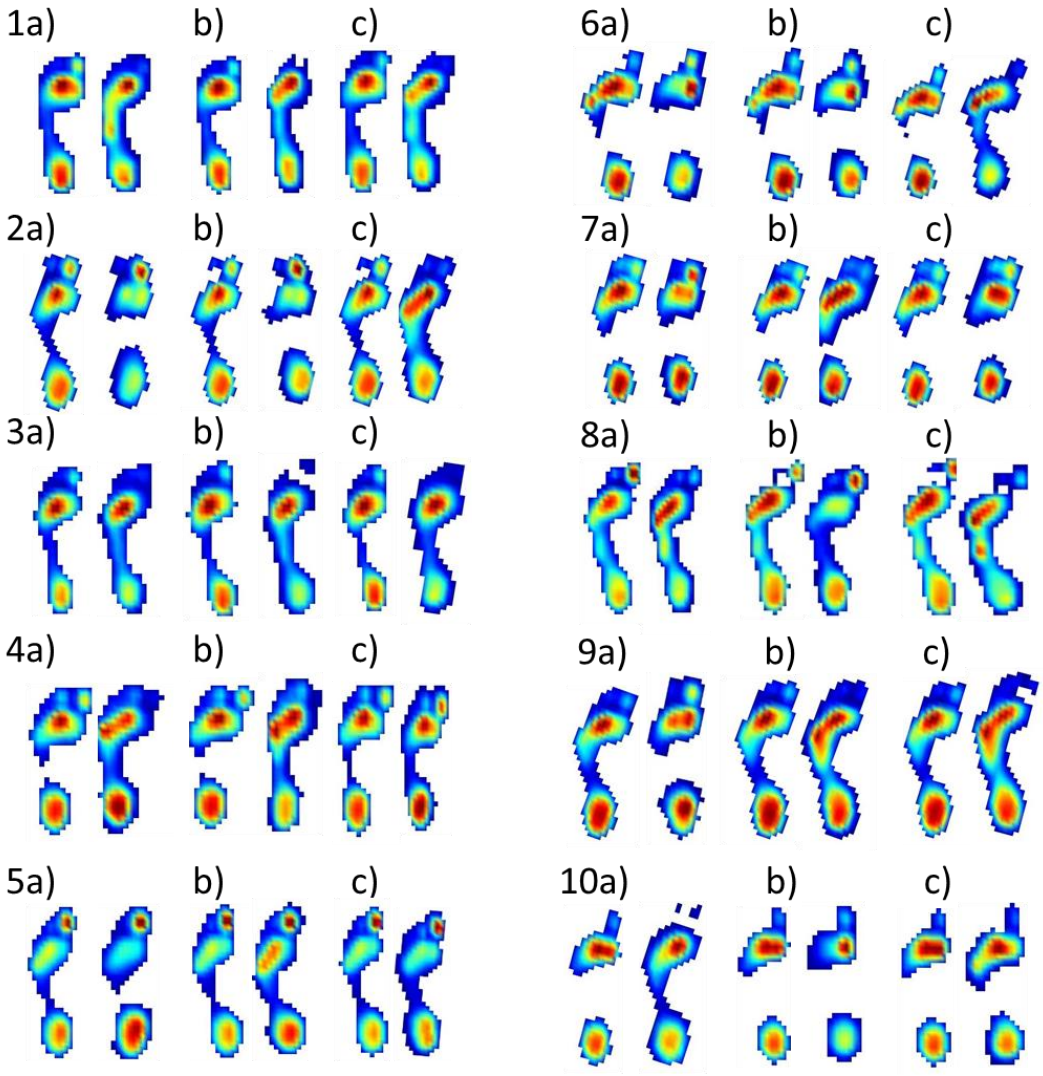

Figure 3.6: Example foot prints for each of the 10 subjects (1-10) during smooth pursuit tracking against each clutter level (a = blank scene; b = savannah scene; and c = forest scene). The prints represented in each set are the mean (left) and the print with the highest mean square error (right).

3.3.2 Repeatability

Repeatability analysis was conducted on subject 9 to ensure data was reliable and representative. The subject repeated the exercise for each of the six combinations of visual tracking type and visual clutter level (both gaze fixation and smooth pursuit on plain, savannah, and forest scenes) five times. Variance in foot pressure mean square error (MSE) in each case demonstrated relative consistency across repeats 1-4, however variance values for repeat 5 were consistently low when compared to the other repeats (Table 3.1).

Combination	Repeat 1	Repeat 2	Repeat 3	Repeat 4	Repeat 5
B/GF	16.00	18.55	18.53	16.49	13.77
B/SP	14.54	18.54	20.29	17.99	10.74
S/GF	10.74	10.01	12.17	11.60	9.37
S/SP	10.37	14.04	12.66	14.40	9.32
F/GF	11.24	11.47	10.71	13.23	8.26
F/SP	14.46	12.65	10.53	15.44	6.60
Mean	**12.89**	**14.21**	**14.15**	**14.86**	**9.68**
SD	**2.39**	**3.61**	**4.20**	**2.29**	**2.43**

Table 3.1: Repeatability of variance in foot pressure MSE for each combination of tracking type (GF = gaze fixation, SP = smooth pursuit) and clutter type (B= blank, S= savannah, F= forest) in subject 9. Means and standard deviations are reported for each combination of tracking type and visual scene, and for each repeat.

A repeated measures ANOVA demonstrated within-combination differences in variance in mean foot pressure MSE across the repeats (F (4, 20) = 8.818, $p <$ 0.01). A post-hoc pairwise comparison following Bonferroni correction indicated that this significance was the result of repeat 5, with variance in foot pressure values in repeat 5 (9.67 ± 2.43) significantly lower than those recorded during repeat 4 (14.86 ± 2.29) (p = 0.04). No other significant within-combination-differences were recorded (Figure 3.7).

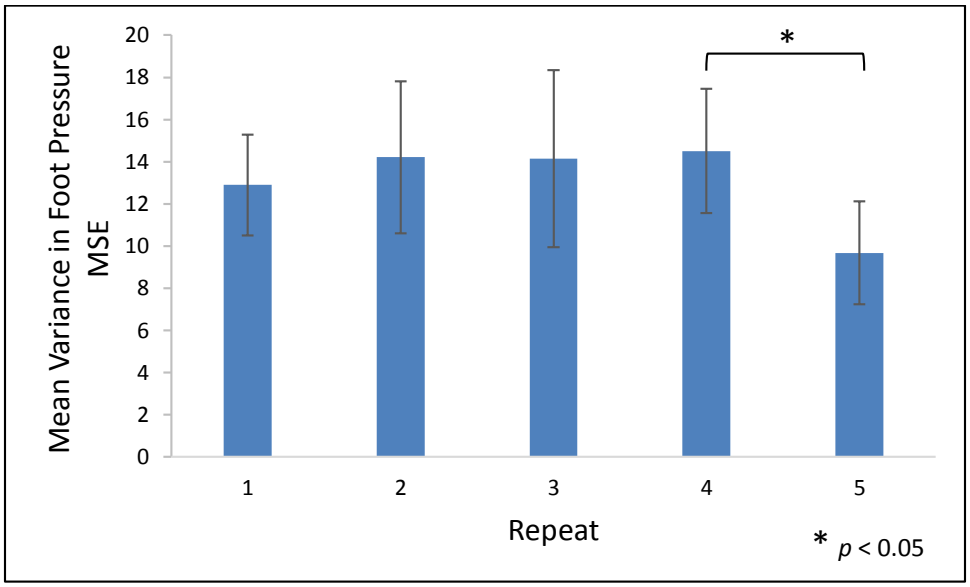

Figure 3.7: Comparison of variance in foot pressure mean square error (MSE) between repeats.

Because of the fact that no other significant differences were observed between repeats, it is possible that a confounding factor contributed to the lower levels of foot pressure variability observed across the final repeat. This could include slight alterations in ambient light or noise levels outside of the experimental area that were difficult to control, or indeed at this point the number of prior repeats may have been sufficient to improve confidence and performance with the task even with the considerable time gaps between repeats.

Further, the very fact that within-subject effects of tracking type were not significantly different across the single repeat of trial combinations conducted for all subjects suggests relative consistency of foot pressure variability (Figure 3.8). Therefore, the single set of trials conducted for each subject was deemed representative.

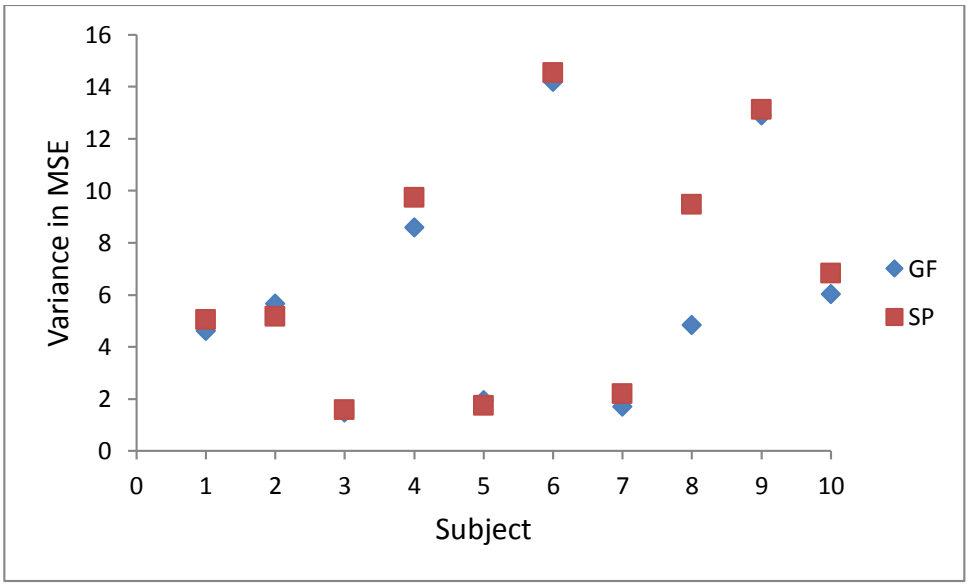

Figure 3.8: Comparison of the mean variance in foot pressure mean square error (MSE) when tracking an object with gaze fixation (GF) or Smooth Pursuit (SP). Values represent the mean variance derived from individual values across all levels of visual clutter.

3.4 Discussion

The fact that foot pressure variability did not appear altered by visual tracking complexity is intriguing given the differences in neuroprocessing demand between smooth pursuit and gaze fixation. This suggests that modern humans are adapted for complex visual environments, and in particular dealing with moving visual stimuli. The results do however show a clear effect of background clutter level on foot pressure variability during visual tracking. Contrary to the hypotheses, it appears that a lack of visual referents rather than larger levels of visual clutter induces an increase in foot pressure variability. Indeed, these results might suggest that when tracking using smooth pursuit against the savannah and forest backgrounds the static features could compensate for body motion induced by tracking the moving target by enabling postural control to utilise static 'anchors'. Such anchors were not provided to the same extent within the blank background, and hence postural control would have remained strongly coupled to the moving visual target. This could therefore explain why postural control was significantly reduced when gaze tracking in this

instance. This work therefore supports previous descriptions of the benefits of sensory anchors, including visual, by Meyer and colleagues (Meyer et al., 2013).

Indeed, in terms of the mechanics of the eye movements involved in gaze tracking, it is known that smooth pursuit eye movements are continually interrupted by saccadic movements that search the visual field for referents, and make smooth tracking less effective (Collewijn and Tamminga, 1984). It has also been shown that reference objects in backgrounds, even simple dots, can improve efficiency of smooth pursuit eye movements by providing necessary information about the target position relative to the background (Brenner et al., 2001). Therefore, there appears to be a benefit to these static visual referents in providing stable reference points for postural stabilisation, and also through improved efficiency and reduced cognitive demands of smooth pursuit movements.

However, in the relative absence of these referents when tracking against the blank background, automatic postural responses are likely to have to drive larger numbers of corrective movements due to the more disruptive and less stable visual input. For example the more diffuse pressure distribution under the forefoot seen in the most variable prints during smooth pursuit tracking is consistent with, and thus may in turn result from, a so-called 'lateral ankle strategy' (Hof et al., 2010, Hof et al., 2007, Hoogvliet et al., 1997) that modulates foot rollover, and is the main balance strategy during single support. This strategy involves the contraction of muscles around the subtalar joint that induce a shift of centre of pressure under the foot and generate a stabilising moment of force to counteract unwanted body tilt (Hoogvliet et al., 1997). Other muscle synergies such as the hip strategy may also be at play in activating the hip extensors and flexors to maintain position of the centre of mass (Shumway-Cook and Woollacott, 2000b). Hence, the variability seen in foot pressures may reflect utilisation of the lateral ankle strategy and other motor synergies, particularly during the more vulnerable single support phase of the gait cycle, in order to support the head and maintain visual acuity.

However, it should be noted that as this study utilised only static backgrounds for the visual tracking task, the potential impact of moving objects in the visual field has not been taken into account. It is suggested that the presence of movement in the visual field in itself is likely to reduce balance as postural control has to remain coupled to moving visual inputs. However, when also tracking a moving object across a moving visual field, balance is likely to be further compromised as smooth pursuit movements are more disjointed due to distraction from surrounding moving stimuli. Therefore it is possible that visual clutter level may actually have a significant impact when large numbers of moving stimuli are present in the environment, for example in areas of high traffic, although this will require further study.

3.4.1 Implications with Respect to Ageing and the Built Environment

Therefore although smooth pursuit eye movements do not appear to pose any greater threat to postural stability than does gaze fixation, the make-up of individual features in the visual field does appear to impact upon multi-modal integration and postural control. The design and structure of built environments is of particular importance, especially with respect to the elderly and infirm in which it well known that sensorimotor integration is already compromised. The elderly often suffer from poor joint mobility (Freemont and Hoyland, 2007) reducing the independent rotational ability of the head, pelvis, and hips (Chiacchiero et al., 2010, Cinelli et al., 2008, Paquette et al., 2006, Van Emmerik et al., 2005), and as a result elderly people are often deliberately more cautious, using strategies such as reducing step length and velocity, and increasing step width to counteract fear of falling (Paquette et al., 2008, Fuller et al., 2007).

Alongside this, reduced visual function with ageing is known to alter eye movement control (Knox et al., 2005, Spooner et al., 1980, Sharpe and Sylvester, 1978). It has been shown that visual decline directly contributes to falls (Abdelhafiz and Austin, 2003, Ivers et al., 2000, Grisso et al., 1991) and

smooth pursuit eye movements in particular have a reduced gain (Spooner et al., 1980, Sharpe and Sylvester, 1978) and an increased lag time (Knox et al., 2005, Sharpe and Sylvester, 1978) in the elderly. Under normal circumstances the sub-clinical symptoms of ageing do not affect function as long as the CNS can compensate (Woollacott, 1989), however it is well known that the elderly have trouble allocating attention to additional tasks (Shumway-Cook and Woollacott, 2000a, Teasdale et al., 1991).

This is of particular concern given the complex nature of modern environments where attention often has to be divided across several tasks. It is therefore vital that the design of such environments takes into account the sensorimotor decline typical of ageing in order to maintain the wellbeing of elderly individuals (Frank and Patla, 2003). Whilst the results of this study suggest that there is unlikely to be much difference in postural control amongst medium and high level visual clutter in young, healthy subjects, this may not be the case for the elderly. Indeed, their sensorimotor deficits are likely to make sensorimotor integration in visually complex environments more difficult to some degree. The results from this study also stress the importance of an adequate number of static visual referents that act as postural anchors even in young, healthy subjects. Such anchors are likely to be of greater importance to the elderly in which postural sway is already increased. Studies have also shown similar benefits to postural control of auditory and tactile postural anchors (Meyer et al., 2013), and hence relatively simple environmental features could help maintain balance in complex environments. For instance, in areas with high-speed traffic flow, larger and clearer signage, hand railings, and improved lighting and auditory cues, are all likely to help maintain balance in elderly individuals in their own right. However, when combined with traffic calming measures to slow down the traffic this would also allow elderly subjects more time to process the presence of, and deduce the speed of, oncoming vehicles. Consequently, older individuals are not only likely to be less prone to falls, but are also less likely to make poor judgements, providing a dual benefit to postural control and safety.

3.4.2 Implications for Evolution and Sensorimotor Adaptation

The implications of these results are not just applicable to modern humans however, but potentially provide considerable insight into how our ancestors came to be able to utilise smooth pursuit at no extra cost to stability. It is probable, just as in modern humans, that performance of smooth pursuit was related to environment and training and it is likely that the endurance running and persistence hunting capabilities thought to characterise *Homo erectus* (Liebenberg, 2006, Bramble and Lieberman, 2004, Carrier et al., 1984) in particular played an important role in selecting for effective smooth pursuit.

However, recent reconsideration of morphological differences between australopiths and early *Homo*, including leg length and body size, suggest that differences in body proportions once considered to be pronounced, may in fact be more nuanced (Antón, 2012, Holliday, 2012, Pontzer, 2012). This in turn suggests that biomechanically the late australopiths may have been much similar than previously thought to early *Homo* in their capabilities. As the results of this study suggest that postural control may not have been significantly threatened in forest environments when compared to more open environments, it is possible that selection for efficient tracking against high levels of visual clutter in australopiths increased sensorimotor integration capabilities. This is supported by the fact that some of the first evidence of the defleshing of animal bones comes from cut marks on bovid bones associated with *Australopithecus garhi* (Semaw, 2000, De Heinzelin et al., 1999), a species known to inhabit both woodland and open grassland environments, and a species suggested as a possible ancestor of *Homo* (Asfaw et al., 1999).

Evidence suggests that the inferior parietal lobe, a region of the brain known to be involved in diverse auditory-motor (Price, 2010, Pa and Hickok, 2008) (Pa and Hickok, 2008, Price, 2010) tactile-motor (Eickhoff et al., 2006, Blakemore et al., 1998) and visual-motor (Creem-Regehr and Lee, 2005, Johnson-Frey et al., 2005) transformations, is particularly important in tool use.

Consequently, the training and optimisation of processing in such areas associated with the visually complex forest environments may have optimised multimodal integration abilities and allocation of attention. This may therefore help to explain why hominins that had yet to benefit from the large increase in brain size and encephalization seen in *Homo* from 500 Ka onwards (see e.g. Antón, 2003), were able to develop not only tool use, but cultural style in tool manufacture: clearly evinced in Acheulian industries from as much as 1.76 Ma (Lepre et al., 2011).

3.4.3 Conclusion

This study set out to assess how visual tracking impacts on foot pressure variability during treadmill walking in young healthy subjects. It has demonstrated that young healthy humans are under no increased risk to stability when walking and performing more complex smooth pursuit eye movements. It is likely that this reflects a high degree of adaptation to tracking moving stimuli, including predator or prey animals, in our evolutionary history, and the large numbers of pedestrians and traffic typical of modern day life, and the optimisation of neural processing we have acquired as a result. Smooth pursuit was however seen to be affected by clutter levels, with increased variability in foot pressures seen against the blank background with the lowest level of visual clutter. It is inferred that this is a consequence of the need for sufficient static referents in the visual field from which to deduce information about target position and speed. With increasingly urban environments this has clear implications for the design of areas where multi-sensory integration is vital, such as pedestrian crossings. This is particularly important given our rapidly ageing population, with the associated increase in sensory deficits and fall risk. The relationship of smooth pursuit and clutter levels could also however provide insight into how the optimisation of multi-modal integration contributed to the initial development of cognitive abilities long before substantial increase in brain size (which began some 500 Ka) allowed for more human–like cognition.

Chapter 4: The Impact of a Dual Visual-Auditory Task During Walking

4.1 Introduction

During movements made in response to the environment, vision is combined with sensory feedback from the vestibular and proprioceptive systems to yield an overall sense of balance and position of the body in space. Maintaining stability during walking is therefore a complex, multi-dimensional process: it requires higher level motor control in order to enable adequate response to threats and cues in the environment, whilst other cognitive tasks are performed concurrently (Buchman et al., 2011). Under normal circumstances, the resulting competition between the attentional demands of walking and the concurrent task do not affect function as long as the CNS can compensate (Woollacott, 1989). However, when processing capabilities are exceeded, sensory inputs must be prioritised (up-weighted) or de-emphasised (down-weighted) according to the most immediate need (Schweigart and Mergner, 2008, Paige, 1994b). This often results in one task being performed at the expense of another: for instance, recent studies suggest that postural control acquiesces to active visual tracking and potentially to gaze fixation (Logan et al., 2010). This suggestion has important implications given the nature of urban environments, where attention often has to be divided between several tasks. For instance, even the simple act of talking has been shown to affect gait while walking (Lundin-Olsson et al., 1997).

Dual-task related gait changes have been shown to include an increase in stride-to-stride variability (Taylor et al., 2013, Beauchet et al., 2005), a decrease in stride length (Donoghue et al., 2013, Simoni et al., 2013, Taylor et al., 2013, O'Shea et al., 2002), and decreased walking speed (Donoghue et al., 2013, Simoni et al., 2013, Taylor et al., 2013, Beauchet et al., 2008, O'Shea et al., 2002) when performing an attention-demanding task compared to walking alone. These changes to gait patterns, particularly decreased gait-speed, are

thought to be the result of a deliberate strategy to avoid loss of balance. For instance, decreased stride velocity has been shown to be the consequence of increased stride time, which in turn has been linked to an increase in the length of the double support phase (Beauchet et al., 2005). This may therefore reduce attentional demand during the more vulnerable swing phase, and minimise risk of imbalance (Beauchet et al., 2005, Woollacott and Shumway-Cook, 2002)

Exploring the impact of these observed effects is of particular importance due to the strong relationship between the afore-mentioned changes and the risk for falling. Decreased gait speed (Beauchet et al., 2008, Bootsma-van der Wiel et al., 2003, Lundin-Olsson et al., 1997) and increased stride to stride variability (Bloem et al., 2003) in particular have been associated with falls. Increased fall-risk is particularly likely in the elderly, in which difficulty allocating attention to additional tasks (Shumway-Cook and Woollacott, 2000a, Teasdale et al., 1991), and hence the challenge of dual-tasking, is further increased as a consequence of age related deficits in both cognitive and motor abilities.

As such, research to date has mainly focused on the elderly and infirm (Donoghue et al., 2013, Simoni et al., 2013, Taylor et al., 2013) as those primarily at risk in dual task scenarios, and hence the impact of dual tasking in young, healthy subjects is less well known. However, although young, healthy subjects may be more able to integrate multiple modalities efficiently, there are still likely to be changes to gait patterns as a consequence of task prioritisation. In particular, studies have so far been unable to assess how underfoot pressure distributions may change in these conditions, and have focused on stride-to-stride variability and gait velocity parameters (Donoghue et al., 2013, Simoni et al., 2013, Taylor et al., 2013, O'Shea et al., 2002). Indeed, considerable intra-subject variability in foot pressure distribution patterns has been demonstrated during normal walking in young, healthy subjects (Bates et al., 2013b), and hence the impact of dual tasking on the gait of such individuals certainly warrants attention. In addition, the interactions between multiple tasks which are far more typical of real-life scenarios, for example the simultaneous tracking of

objects in the visual environment, and talking whilst walking, are yet to be fully established. For instance, studies to date have utilised cognitive tasks such as backwards counting exercises (Taylor et al., 2013, Doi et al., 2012), or alternate alphabet letter recital (Donoghue et al., 2013, Simoni et al., 2013) that, whilst eliciting a speech response, are not truly representative of day to day speech responses in natural situations: i.e. they may require more concentration and hence a larger attentional load than more naturalistic everyday conversation.

The processing of language is indeed complex, with language relevant cortex extending over both the inferior frontal gyrus (Pulvermüller and Fadiga, 2010, Hagoort, 2005), and the inferior parietal lobule (Pa and Hickok, 2008). Alongside its' role in interpretation and production of phonetic, syntactic, and semantic structure (Pulvermüller and Fadiga, 2010, Hagoort, 2005), the inferior frontal gyrus is also known for its' involvement in the processing of several non-vocal behaviours including visual search (Fink et al., 2006). Further, the inferior parietal cortex is known for its' diverse roles in visual-motor (Creem-Regehr and Lee, 2005, Johnson-Frey et al., 2005) and auditory-motor (Price, 2010, Pa and Hickok, 2008) responses. Consequently, such regions are under large processing loads during dual task scenarios in order to produce appropriate responses for visual and auditory tasks conducted while walking.

However, despite the complexities of this multimodal integration, the benefits of training may have a positive impact on stability by optimising cognitive processing. For instance, there is evidence to suggest that the effectiveness with which smooth pursuit eye movements are carried out in gymnasts when compared with controls demonstrates how enhancements of these eye movements can be seen with regular training (Von Lassberg et al., 2012). This not only enables the neuroprocessing and control of these eye movements to be optimised, but could also indirectly benefit stability in itself by reducing demand on multimodal integration. In such individuals, this may thereby allow for efficient allocation of attention to both cognitive tasks and

postural control, hence posture may be less likely to be affected during dual task scenarios.

By deploying a pressure sensing treadmill utilised alongside a binocular gaze tracking system, this study therefore aims to assess the impact of combined visual and auditory tasks of varying difficulty on foot pressure variability while walking, and hence in turn, their effects on balance and stability.

It was expected that when comparing the impact of two auditory stimuli during smooth pursuit object tracking, foot pressure variability would be larger when the stimuli required a speech response when compared to a background stimulus due to increased processing demand (Hypothesis 1). It was also expected that that, if smooth pursuit tracking was made more complex with the addition of a more complex visual background, these effects on foot pressure variability would be further exacerbated as cognitive load further increased due to excessive visual stimuli (Hypothesis 2). Finally, professional gymnastics training was expected to have a positive impact on minimising the effects of attentional load on foot pressure variability when compared to cardio training or non-professional sports training, due to specific training of eye movements and motor control of balance (Hypothesis 3).

4.2 Methods

4.2.1 Subjects

Ten healthy subjects participated in this study. In order to participate, subjects had to be free from known neurological and musculoskeletal disorders, amongst other limitations. All subjects had normal or corrected-to-normal vision. Ethics approval was obtained from the University of Liverpool Research Ethics Committee (RETH000888), with all subjects giving informed prior consent.

4.2.2 Experimental Setup

Foot pressure data were collected from a Zebris FDM-THM foot pressure sensing treadmill (Isny im Allgäu, Germany) at a frequency of 100 Hz. Pupil movement data was synchronously captured using a binocular eye-tracking system, ViewPoint BSU07 USB-60x3, Arrington Research (Scottsdale, AZ, USA) sampling at 60Hz. An LCD projector, NEC NP2250 (Berkshire, UK) was used to project visual targets on to a curved projection screen, Beamax A-Velvet (Overpelt, Belgium) positioned 2m directly in front of the treadmill so as to prevent distractions from peripheral vision (see Figure 4.1).

4.2.3 Protocol

Subjects walked on the pressure sensitive treadmill at a set speed of 1.1. m/s^{-1} whilst tracking the movement of a dot shaped visual target projected on the screen. This speed was chosen as all subjects confirmed they felt secure walking at this speed and, as demonstrated by their eye tracker profiles (see below), were able to track the target efficiently. Further, the speed is also comparable with those seen of natural walking in young adults (0.71-1.76 m/s^{-1} (42.76 - 105.57 m/m^{-1}) (Waters et al., 1988). The target alternated between stationary phases and periods of movement in order to initiate gaze fixation and smooth pursuit respectively. The sequence lasted for three minutes, and included three stationary phases lasting 20 seconds each, and three movements lasting 40 seconds each. The subjects were made aware of the fact that the target would cycle between stationary phases and movement, the only instruction given being to track the object at all times. They were encouraged to walk and move freely as they would normally, taking into account the constraints of the treadmill environment. To prevent learning and anticipatory smooth pursuit movements, the path of the target varied with each movement.

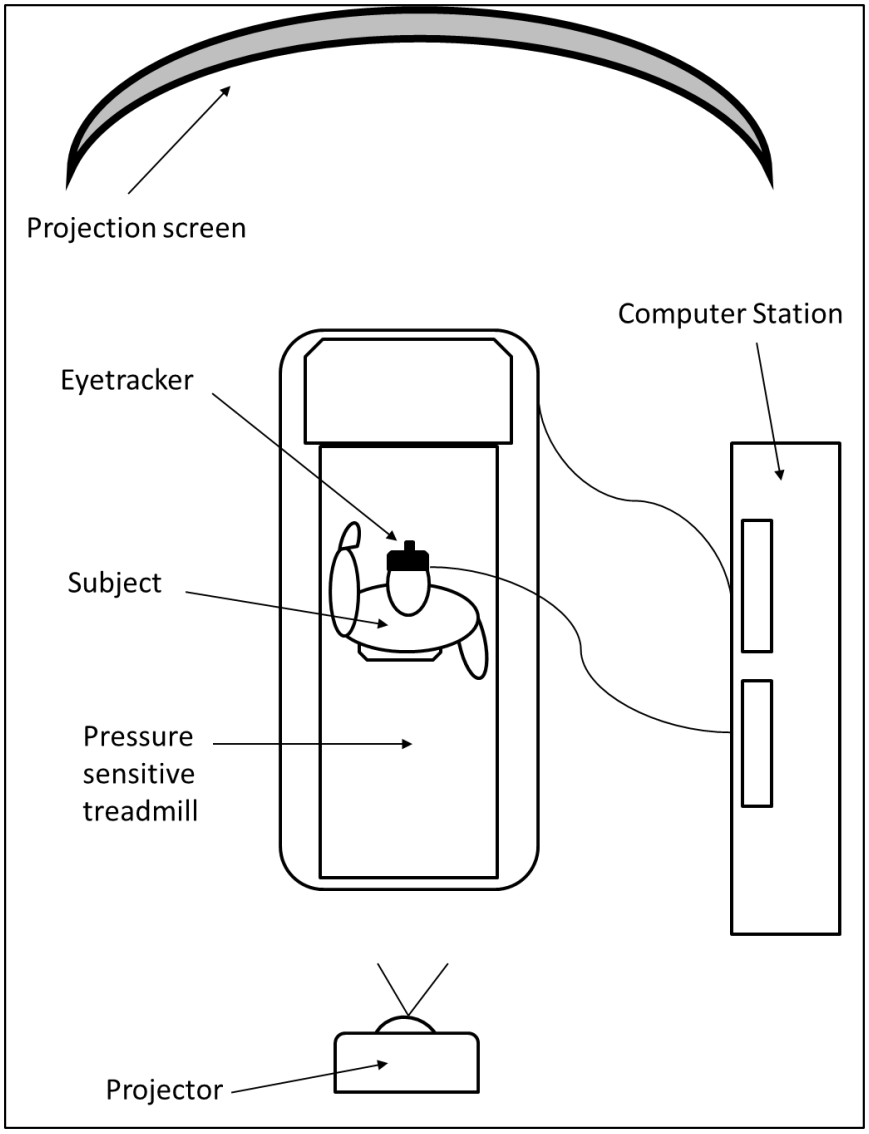

Figure 4.1: Diagrammatic representation of experimental set up, including the eyetracker, pressure sensitive treadmill, projector, and curved projection screen.

In order to assess hypothesis 1, subjects first completed this tracking task across a simple savannah background (see Figure 4.2), and in the presence of two forms of auditory stimuli, delivered through a personal mp3 player and noise-cancelling headphones. These tasks involved a repeat-back language exercise and listening to a piece of background music. For the first trial, the repeat-back language trial, the subjects were played a sequence of clips in a variety of languages (French, Italian, and Spanish). Each consisted of

a short phrase in English followed by a translation, subjects being asked to repeat the translation as they heard it. Phrases were sourced from podcasts created as beginner guides to stock phrases for holidaymakers (http://www.thomson.co.uk/editorial/podcasts/foreign-phrases.html), and were purposely chosen to ensure relative simplicity of pronunciation and shortness of phrase. Each phrase was individually excised from the podcasts using an online Mp3 cutter (http://mp3cut.foxcom.su/en/). For the second trial, the background music trial, subjects were played 'Well-Tempered Clavier, Book 1, Prelude No.1 in C major BWV846' by Bach, chosen due to the monotonicity and consistent rhythmic pattern.

For hypothesis 2, the two trials were repeated as above but the tracking background was changed to a more complex and visually cluttered forest scene (see Figure 4.2).

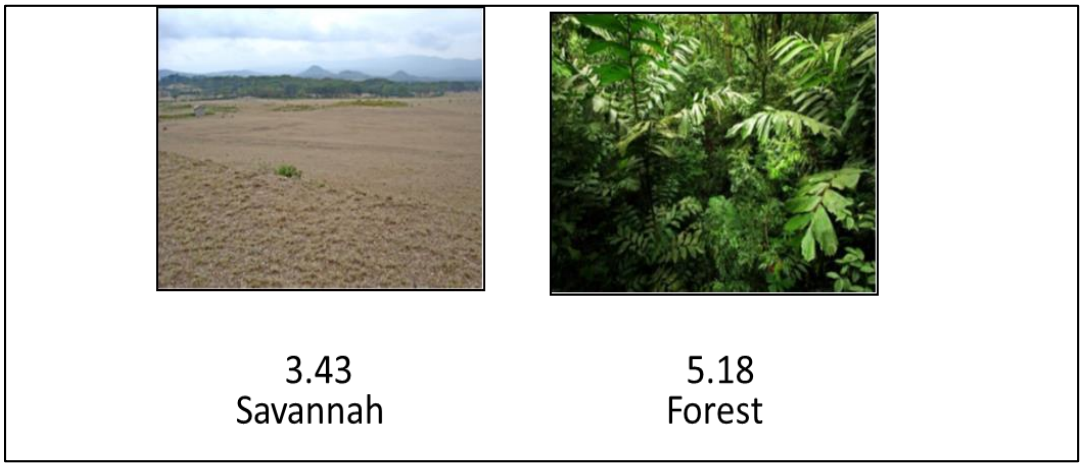

Figure 4.2: Background images representing the two visual clutter levels tested. Values represent quantitative estimation of clutter generated using the code of Rosenholtz et al. (2007) as in Chapter 3).

To ensure that the complexity of the backgrounds were quantitatively different, both the savannah and forest images were assessed using the code of Rosenholtz et al. which used the principles of feature congestion to provide values for the visual clutter levels in each image (Rosenholtz et al.,

2007)(Figure 4.2). Throughout all data collection, the experimental area was kept clear of any non-experimental visual and auditory stimuli so as not to distract the subject from the task. This included prevention of any movement of, or communication between, researchers and other staff present in or adjacent to the experimental area by means of a 'warning light' in use throughout each trial.

4.2.4 Data Analysis

For each trial, pupil movement data captured by the eye tracker was imported into MATLAB (MathWorks, USA) to confirm that efficient object tracking had taken place (see Appendices A3.1-A3.10 for eye tracking profiles for each subject). For any trials in which the eye tracking profile was unsatisfactory, for instance where the pupil movement was particularly erratic and noisy, or it was clear that it had not tracked the target in the X plane, the data were discounted and the trial repeated. The movement of the pupil in the X plane was plotted as a line graph, enabling the bouts of gaze fixation and smooth pursuit of the trial to be clearly segmented (Figure 4.3). The start and end points of each bout were marked by plotting cross hairs on the profile, and using in-house code (Appendices A1.2 and A1.3) the foot pressure records obtained during the marked-off sections were then identified and grouped (A1.4 – A1.6).

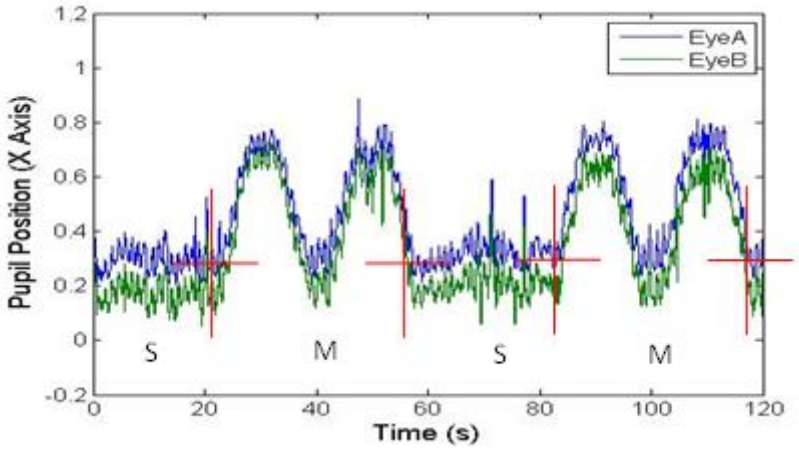

Figure 4.3: Exemplar eye tracking profile showing horizontal pupil movement. Segments marked 'S' indicate the portions of the trial where the target is stationary and gaze fixated. Segments marked 'M' indicate areas of target movement, and hence Smooth Pursuit (SP) occurrence. Red bars indicate transitional points, a buffer around which discounted any pressure records made during transitional phases.

So as to prevent the inclusion of any records made during the transition between gaze fixation and smooth pursuit, a 2 second exclusion zone was put in place either side of the cross hairs.

This yielded a group of foot pressure records made during smooth-pursuit tracking for each of the four conditions in each subject (40 groups in total). The foot pressure record groups so identified were then analysed using an in-house software toolkit, pedobarographic Statistical Parametric Mapping (pSPM) (Pataky et al., 2008) (Appendices A1.7 and A1.8). This technique, derived from algorithms originally developed for use with images produced during functional magnetic resonance imaging (fMRI) (Friston, 1997), 'fits' each foot pressure record to all others in the data set so that structures optimally overlap, enabling comparisons to be made between them at the pixel level.

4.2.5 Statistical Analysis

Statistical analysis was performed in MATLAB (MathWorks, USA) and SPSS (IBM, UK). Firstly, mean square error was calculated for each pressure record within each group to quantitatively define how each record differed from the mean. The variance in mean square error for each group was then

calculated and used as a measure of overall variability for the foot pressure records within the group (See Appendices A3.11 - A3.20 for diagrammatic representations of foot pressure mean square errors for each subject). A repeated measures ANOVA was conducted following Bonferroni correction in SPSS (IBM, UK) to assess the effects of auditory task type, visual clutter level, and exercise training on foot pressure variability.

4.3 Results

A repeated measures ANOVA was used to assess the impact of the dual visual and auditory task on foot pressure variability during walking. Comparisons of within-subject variance in foot pressure mean square error with respect to the blank, savannah, and forest visual scenes (16.01 ± 5.32, 14.46 ± 3.40, and 13.82 ± 4.22 respectively) demonstrated an insignificant effect of visual clutter level (F (2, 14) = 0.78, p = 0.48) (Figure 4.4).

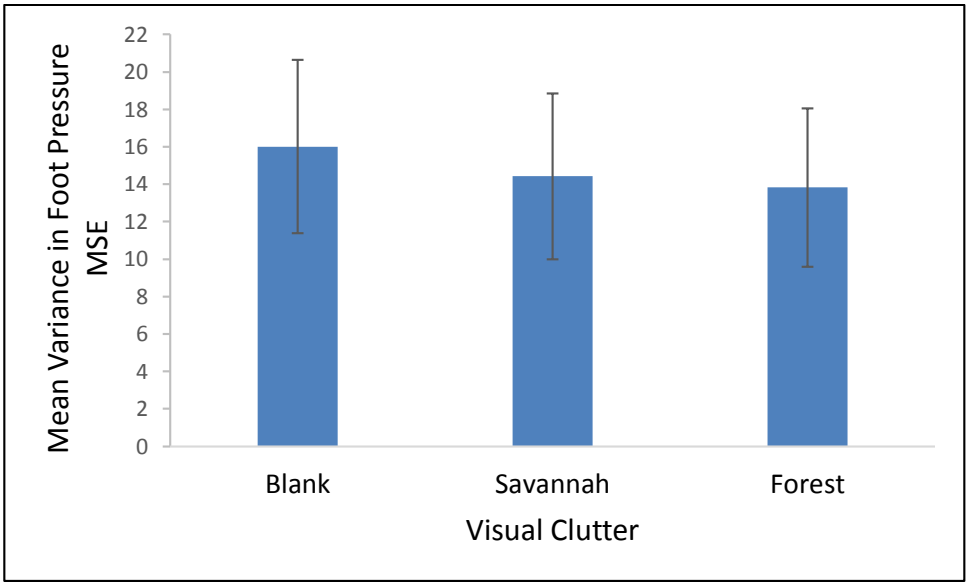

Figure 4.4: The effect of three different clutter levels on variance in foot pressure mean square error (MSE) during a dual visual-auditory task.

However, the effect of auditory task did have a significant impact on variance in foot pressure mean square error, with larger variability in foot pressure mean square error observed when undertaking the repeat-back language task (16.90 ± 4.63) when compared to the background music task (12.62 ± 3.92) (F = (1, 7) = 17.66, p = 0.004) (Figure 4.5).

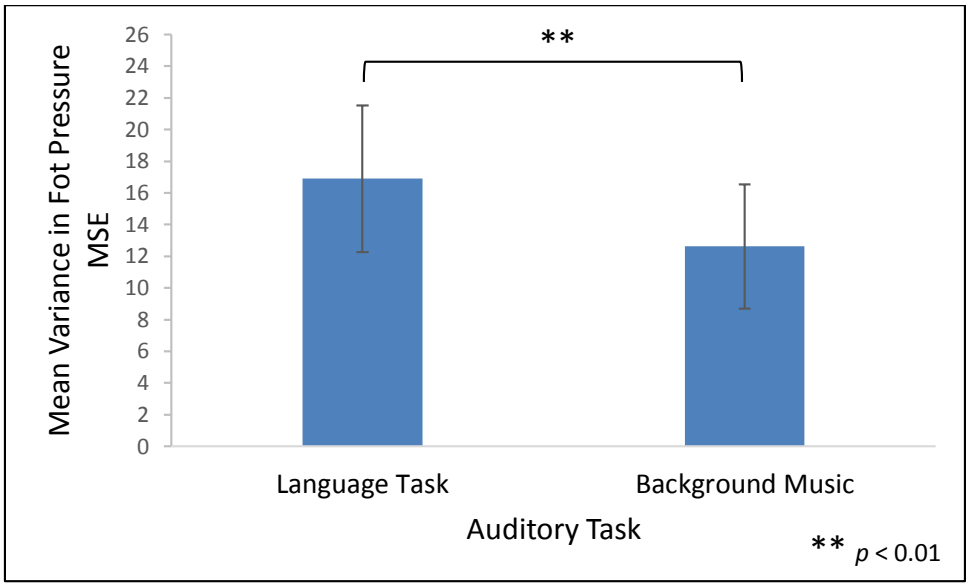

Figure 4.5: The effect of two auditory tasks on variance in foot pressure mean square error (MSE) during a dual visual-auditory task.

To assess further how foot pressures varied during the different auditory tasks, a visual comparison of the mean print to the most varied print provides a qualitative impression of how foot pressure might vary with each auditory task (Figure 4.6). This indicates that under-heel pressure remains relatively constant, and that the differences expressed in the most variable prints are under the forefoot. These changes in underfoot pressure range through a more diffuse pressure across the lateral forefoot and midfoot (seen e.g. in subjects 2-4, 6, 7 and 9), and a shift in pressure under the medial forefoot and hallux (seen e.g. subjects 5 and 8).

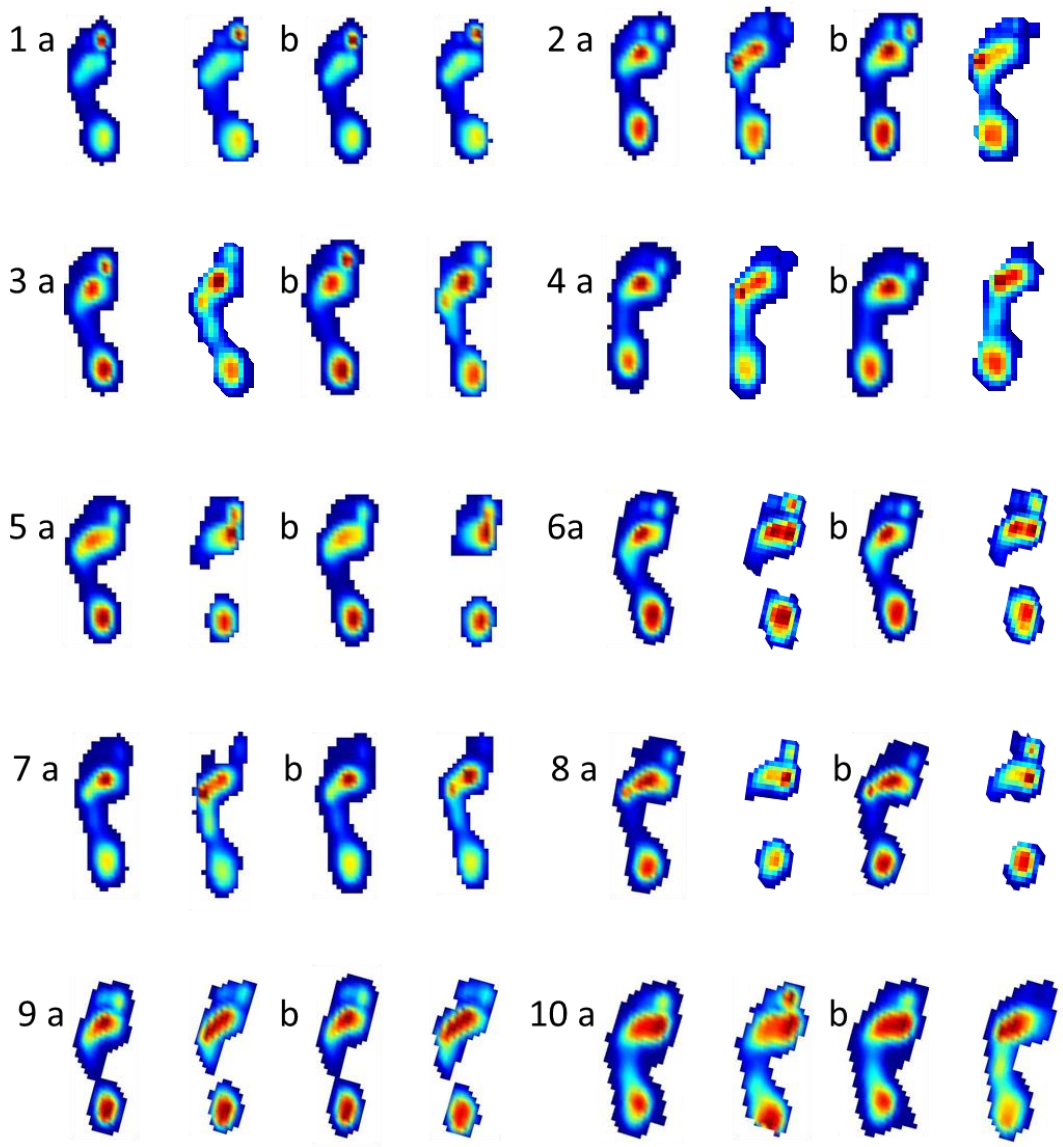

Figure 4.6: Example foot pressure records for each of the 10 subjects (1-10) during smooth pursuit tracking against the savannah scene when listening to music (a) or completing the language task (b). The prints represented in each set are the mean (left) and the record with highest mean square error (MSE) (right).

4.4 Discussion

Considering the impact of dual tasking when walking, these results demonstrate clearly, and as hypothesised, that there is significantly higher

variability in foot pressure patterns when tracking a visual object with the addition of a more complex auditory task (repeat-back language task) when compared to a simpler auditory task (listening to background music).

Although seemingly requiring different sensory modalities - speech being centred around auditory and vocal modalities, and visual tracking being centred around predominantly the visual and proprioceptive modalities - the neural pathways involved in both tasks converge on the same areas of the brain. One of these regions is the inferior parietal lobule, a region of the brain known to be involved in diverse auditory-motor (Price, 2010, Pa and Hickok, 2008) and visual-motor (Creem-Regehr and Lee, 2005, Johnson-Frey et al., 2005) transformations. This not only includes the dorsal stream that controls eye movements (including those made during smooth pursuit), and the guidance of actions in response to vision (Goodale and Milner, 1992), but also vocal perception, imitation and production (Price, 2010, Peschke et al., 2009, Pa and Hickok, 2008). Information from the inferior parietal lobule is communicated to the premotor cortices of the frontal lobes which are responsible for generating sequential plans to be executed by the primary motor cortex.

The frontal lobes are also associated with executive function and working memory; that is the higher level cognitive processes that include the planning and monitoring of strategies for different actions, and the control, regulation, and active maintenance of task-relevant information in both novel and familiar tasks (Malloy and Richardson, 1994). Hence the performance of the repeat-back language task in particular will have relied heavily on the efficient coordination of the visual and auditory inputs, but also a motor response in the vocal repetition. As a consequence, the inferior parietal lobule will have been subject to a higher level of cognitive load than that experienced when completing the background music task, thereby reducing cognitive resources available for other tasks, including postural control. Therefore it is suggested that during the more complex repeat-back language task that subjects allocated more attention to the required motor response (speech) at the expense of postural control. This led to

more variable foot pressure patterns when compared to the simpler background music task which did not need to be allocated the same degree of attention.

However, it was interesting to note that there was no significant impact of clutter level on foot pressure variability during the dual-task conditions. As the subjects completed the experiments in ascending visual clutter level order, it is plausible that a training effect came in to play i.e. that practice improved the efficiency of processing of the simultaneous tasks. There has been much evidence to suggest that dual-task performance can be improved with practice and training, both in young and older adults (Theill et al., 2013, Lussier et al., 2012, Bherer et al., 2008, Bherer et al., 2006, Bherer et al., 2005, Kramer et al., 1995). Further, both cognitive and physical training have been shown to induce functional changes in brain regions of older adults involved in higher order cognition, including the prefrontal cortex and parietal cortex (Brehmer et al., 2011, Voelcker-Rehage et al., 2011, Voss et al., 2010, Dahlin et al., 2008, Colcombe et al., 2004). It is also possible that a 'ceiling effect' is present, whereby the repeat-back language task alongside smooth pursuit tracking evokes considerable neurological demand in itself, and hence the complexity of the visual scene during smooth pursuit tracking does not further influence postural control.

Indeed, this is supported by the lack of any significant difference in foot pressure variability amongst activity type, indicating that there was no added benefit of professional training in hand-eye sports when compared to cardiovascular sports and non-professionals. This would suggest that any potential benefits of smooth pursuit training in those who take part in sports requiring precise hand-eye coordination might only be of benefit in less complex dual-tasking scenarios because of such ceiling effects.

It is also important to note however, that this study has considered the effects of background clutter level on tracking against static background images only. It therefore remains to be seen if similar results would be observed when object tracking in a visual field made up of multiple moving components. In

situations where there are large numbers of moving objects in the field of view, and particularly if static referents are less frequent, stability might be further compromised as fewer sensory anchors (Meyer et al., 2013) are available to assist with the control of balance.

Across the visual clutter levels, and for both the background music and language tasks, the more variable foot pressure records were characterised by differences in the forefoot and the midfoot, particularly on the lateral side. Therefore, it is concluded that these pressure records reflect the actions of the vestibulospinal reflex in making larger numbers of corrective movements during more disruptive visual tracking. The resulting innervations of muscles of the trunk, in particular, may shift the centre of mass laterally in response to medio-lateral movements, leading to the resulting lateral pressure shift observed under the fore- and midfoot.

Further, such pressure distributions might reflect the utilisation of in-place strategies through muscle synergies. This includes the 'lateral-ankle strategy' that modulates foot rollover, and is the main balance strategy during single support (Hof et al., 2010, Hof et al., 2007, Hoogvliet et al., 1997). This strategy involves the contraction of muscles around the subtalar joint that induce a shift of centre of pressure under the foot and generate a stabilising moment of force to counteract unwanted body tilt (Hoogvliet et al., 1997). It also includes the hip strategy that alters underfoot pressure distribution via activity of the flexors and extensors of the lower legs. Hence, the variability seen in foot pressures may also reflect the utilisation of both of these strategies, particularly during the more vulnerable single support phase of the gait cycle.

4.4.1 Societal and Clinical Implications

This research therefore has clear implications for those in whom cognitive deficits are common. For example, it is noted that the elderly often have difficulty allocating attention to additional tasks (Shumway-Cook and Woollacott, 2000a, Teasdale et al., 1991). Further, the elderly have been observed to possess a reduced postural reserve, the term used to define an

individual's ability to respond to postural threat (Yogev-Seligmann et al., 2008). As such, if a concurrent task becomes too complex, one task must be prioritised over another. This often results in one task being performed at the expense of another: for instance, elderly subjects may stop talking while walking (Lundin-Olsson et al., 1997).

Age-related changes in both the morphology and function of the brain have been known since the 1990s (Raz et al., 1997, Malloy and Richardson, 1994) and with recent advances in functional magnetic resonance imaging (fMRI), are becoming even easier to observe (Brehmer et al., 2011, Voss et al., 2010, Raz et al., 2005, Raz et al., 1997). It is known that the cerebral cortex degrades with age, resulting in both a reduction of grey and white matter in the pefrontal cortex and also a reduction of mass in the frontal lobe (Park and Reuter-Lorenz, 2009, Raz et al., 2005, Raz et al., 1997). Because the frontal regions in particular are affected, higher level functions - including executive functions – are most vulnerable. As a result, the extent to which neural plasticity can compensate for age related deficits is limited. It is therefore speculated that when performing concurrent tasks during walking, as required in many aspects of daily life, stability in the elderly and infirm may be further compromised.

Even when dual tasks are successfully performed alongside walking, the allocation of attention to both the cognitive and postural tasks may result in poorer performance on both parts (Yogev-Seligmann et al., 2008). Indeed, several studies of elderly subjects report reduced reaction times (Chen et al., 1996, Ebersbach et al., 1995, Lajoie et al., 1993), or reduced performance (Lindenberger et al., 2000) of a cognitive task while walking. Studies have also observed increased gait variability (Dubost et al., 2006) and a larger number of (Lindenberger et al., 2000) in elderly subjects performing dual tasks while walking. These observed changes to gait patterns may have considerable implications when considering the risk of falls and injury in such individuals, particularly as the elderly are already at increased risk due to their muscle deterioration and weakness (Paterson et al., 2007).

This increased risk is of particular concern with regard to increasingly complex urban environments. Whilst the results of this study have found an insignificant effect of background clutter level on foot pressure variability whilst completing a dual visual-auditory task, the fact that task complexity had an effect on foot pressure variability has implications when considering the complex tasks required of daily life in such environments. For instance, pedestrian crossings pose a particular threat to the elderly who are less able to judge speed of oncoming vehicles, and may much more readily make inappropriate predictions on available crossing time (Zivotofsky et al. 2012), which can lead to falls or inappropriate muscle activations due to time pressure. Furthermore, current road markings and illuminations have been shown to be ineffective, and in some cases may even be harmful (Retting et al. 2003). In crossing situations, attention must be divided between watching and listening for traffic and preparing motor sequences to stop or cross when appropriate, and in the elderly this may be much more difficult due to the deficits described above. Particular care therefore needs to be taken to maximise safety in urban environments through the careful design of environments to optimise sensorimotor integration. Advances in vibrotactile feedback systems suggest that vibratory indications of head and trunk tilt may also help improve confidence and balance and minimise risk of fall and injury (Haggerty et al., 2012, Janssen et al., 2012).

4.4.2 Implications for Evolution and Sensorimotor Adaptation

The implications of these results however are not just applicable to modern humans, but may also provide considerable insight into the evolution of cognitive processing abilities in our ancestors. It is not unlikely that one of the selective forces for the large increase in brain size seen in later *Homo erectus* (Ruff et al., 1997) was the emergence of the persistence hunting lifestyle (Bramble and Lieberman, 2004, Carrier et al., 1984). The need to be able to track moving prey efficiently whilst giving chase is a key example of dual tasking need in our evolutionary history. It is therefore likely to have placed significant selection pressures on the efficiency of visual-motor integration, and hence the ability to process sensory input and consequent motor tasks simultaneously.

The concurrent emergence of further attention demanding tasks such as the increasing sophistication and cultural style in both tool use and manufacture (Lepre et al., 2011) from as far as 1.76 Ma, are also likely to have played a role in the optimisation of neural processing capabilities, especially in dual-task scenarios. For example, the late Acheulean tool-making associated with *Homo erectus* involved the intentional shaping of a bifacial tool (handaxe) using controlled and precise fracture (Asfaw et al., 1992, Isaacs and Curtis, 1974, Leakey, 1971). As it does not just rely on manual praxis, but rather on hierarchical action sequences and the updating of those sequences in response to sub-goals, it is neurologically complex (Stout and Chaminade, 2012). Indeed, it places large demand on anterior portions of the frontal cortex (Badre and D'Esposito, 2009), and increased activation is indeed observed in these areas in modern expert tool makers (Stout et al., 2008). In turn, this larger recruitment of areas of the frontal cortex indicates the increased visuo-motor coordination required of advanced tool-making.

The selection for these capabilities are likely to have played a significant role in hominin brain and cognitive evolution (Stout and Chaminade, 2012). This is further supported by the 'technological pedagogy' hypothesis, which suggests that intentional vocal communication evolved as a consequence of the complex manual praxis required of tool-making having to be inferred rather than simply observed (Stout and Chaminade, 2012), providing a context for imparting knowledge through demonstration (Csibra and Gergely, 2011).

It is suggested therefore, that the development and perfecting of the persistence hunting lifestyle, alongside the development of other cognitively demanding processes such as speech and tool use, are likely to have played a significant role in the optimisation of multi-modal integration. It is proposed that the resulting efficiency of dual tasking in modern humans is, to some extent, a retained adaptation to the reliance of our ancestors on endurance running in the hunting of prey and avoidance of predators and their growing need for social learning and evolving pedagogy.

4.4.3 Conclusion

This study aimed to determine the effects of dual visuo-auditory tasks of varying complexity on foot pressure variability during treadmill walking. It has demonstrated that, even in young, healthy subjects, performing an auditory task requiring a speech response, as opposed to listening to a piece of background music which did not, led to a resulting increase in foot pressure variability. It is likely that the high demand on shared neural circuits, particularly those requiring the planning and execution of motor acts such as the frontal lobes, leads to the acquiescence of postural control as visual and auditory input take priority. Interestingly, the lack of significant benefit of training in sports requiring large degrees of hand eye coordination may highlight a ceiling effect in terms of the effects of attentional load on postural control. This was also supported by the lack of a significant effect of increasing background visual clutter level during the performance of the dual task.

These results may be particularly important given our ever-ageing population, in maximising sensory processing and minimising fall risks in the elderly, particularly in complex urban environments. It could also, however, provide insight into how the development of cognitive abilities in our ancestors may have already begun to optimise multi-modal integration abilities that allow modern humans to cope with the complex day to day situations experienced in modern day life.

Chapter 5: The Impact of Body Segment Coupling During Walking

5.1 Introduction

The coordination of body segments during dynamic movements and their actions in regulating balance and posture require complex motor control. In order to maintain stability during walking, balance must be regulated at two main levels: the balance of the head, arms and trunk about the supporting hip; and the balance of the body's overall centre of mass about the centre of pressure (MacKinnon and Winter, 1993).

Movement and control of the trunk in particular is known to contribute significantly to balance, as well as being the main locomotor organ in vertebrates, producing up to 50% of spatial gain (Fischer and Lehmann, 1998). During the single support phase in particular, balance is particularly threatened by the rotation of the pelvis as the swing leg induces a destabilising torque in what is known as the 'pelvic step' (Ducroquet et al., 1968). In order to counteract this, an opposing axial counter-rotation of the trunk acts to reduce angular momentum about the longitudinal axis (Gracovetsky, 1985).

Others have also argued that the benefits of independent trunk rotations also extend to energetic efficiency, with the trunk acting as an elastic linkage between the upper and lower extremities (Pontzer et al., 2009a). This can be modelled as two rigid segments (the torso and the pelvis) connected by a torsional spring (the waist) (LaFiandra et al., 2002), which therefore enables the storage and release of elastic energy between the segments. Further, axial rotation of the trunk has been shown to have a relative minimum velocity of $1m/s^{-1}$ in modern humans which is energetically optimal for the whole body (Margaria et al., 1963). At this velocity the trunk acts as a resonating pendulum, and consequently, in addition to supporting balance, it requires minimum energetic input.

Trunk counter-rotations are also aided by both passive and active arm swing. Passive arm swing is driven by trunk rotation and the passive mass damper effect of the shoulders (Pontzer et al., 2009) to counteract the angular momentum produced by leg swing with minimal energy. Active arm swing is employed in order to increase the counter-torsional effects of arm swing when the passive component alone is insufficient, particularly when balance is threatened (Pontzer et al., 2009).

The maintenance of stability of the trunk also plays a crucial role in the stabilisation of the head, which in turn stabilises gaze. This is primarily achieved through the action of the vestibulospinal reflex (Gernandt et al., 1959) that induces compensatory body movements to maintain balance after head motion, but is also aided by the vestibulocollic reflex (Outerbridge and Jones, 1971) that counteracts head motion by acting on the neck musculature (Land, 2004). It appears as if trunk motion is critical in attenuating accelerations between the trunk and head in all directions (medio-lateral, anterior-posterior, and vertical), although neck movements may play a lesser role (Kavanagh et al., 2006).

Despite the clear importance of the coordination of the trunk with the head and pelvis however, the exact mechanisms by which these segments interact, both with each other and with the limbs, is unclear. For instance, although many studies have considered inter-segmental control of balance, most consider the interactions of only of the head and trunk (Kavanagh et al., 2005, Land, 2004, Keshner, 2003, Hollands et al., 2001, Stapley et al., 1999), and do not take into account the contribution of the limbs. There are also gender differences to consider, with the female pelvis having been shown to be subject to larger motion and accelerations in the frontal plane (Mazzà et al., 2009, Smith et al., 2002), possibly in an attempt to reduce displacement of the centre of mass (Smith et al., 2002).

While an understanding of the behaviour of individual segments is a prerequisite of analysis of segment interactions, it is suggested that the former are now well enough understood to advance to an analysis of the combined and

synergistic actions of the segments at a whole body level, and their influence on foot-ground interactions. This study contributes to the latter agenda by investigating the impact of decoupling between the head and shoulders, and trunk and pelvis, by artificially recoupling these segments in healthy young people by the use of medical braces.

The hypotheses were as follows: (1) Foot pressure variability will be increased following body segment recoupling, due to the increased action of vestibulospinal and vestibulocollic reflexes, and muscle synergies, in stabilising the trunk and head; (2) Head movements will be restricted in all of the three major planes (pitch, roll, and yaw) as a consequence of head and shoulder coupling; (3) After recoupling the trunk and pelvis, a consequent reduction in shoulder and pelvic rotation will be observed due to the limited motion of the trunk; (4) In an attempt to preserve counter-rotations following segment recoupling, an increase in arm swing and arm abduction will also be observed; (5) Leg swing will be reduced in an effort to decrease step length, aiding maintenance of the stability of the centre of mass. (6) Gender differences in pelvic shape will result in changes in body segment kinematics between the sexes to maintain the same performance of counter-rotations and forward propulsion.

5.2 Methods

5.2.1 Subjects

Ten healthy subjects participated in this study, five male and five female, with a mean age of 21.50 ± 2.80 years, a mean height of 172.21 ±8.76 cm, and a mean weight of 71.19 ± 11.26 kg. In order to participate, subjects had to be free from known neurological and musculoskeletal disorders, amongst other limitations. Ethics approval was obtained from the University of Liverpool Research Ethics Committee (RETH000888). All participants were provided with a participant information sheet and gave informed prior consent.

5.2.2 Experimental Setup

Foot pressure data were collected from a Zebris FDM-THM foot pressure sensing treadmill (Isny im Allgäu, Germany) at a frequency of 100 Hz. Kinematic data were synchronously captured using a 9-unit Qualisys ProReflex motion capture camera system (Gothenberg, Sweden) running at the same frequency (see Figure 5.1 for experimental setup). Qualisys 19mm retro-reflective lightweight markers (Gothenberg, Sweden) were attached using double-sided tape to anatomical landmarks on the subjects, as shown in Figure 5.1. The exact anatomical landmarks (and body segments) chosen for motion capture analysis are detailed in Figure 5.2 and Table 5.1. These markers were then tracked by the camera system, recording their global coordinates, and hence movement, throughout the trials. To ensure foot pressure and kinematic data were synchronous, an external trigger from the treadmill was used to initiate kinematic capture.

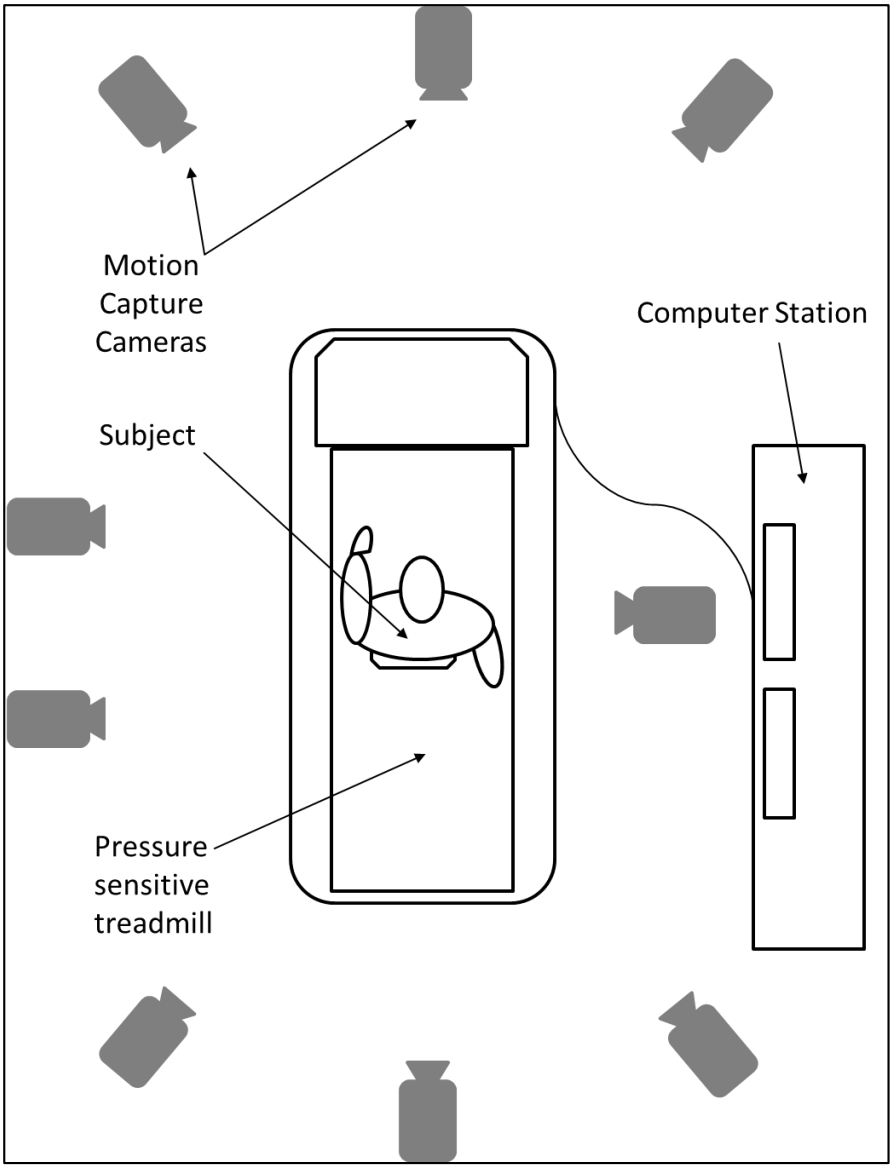

Figure 5.1 Diagrammatic representation of experimental setup including pressure sensitive treadmill, motion capture camera system.

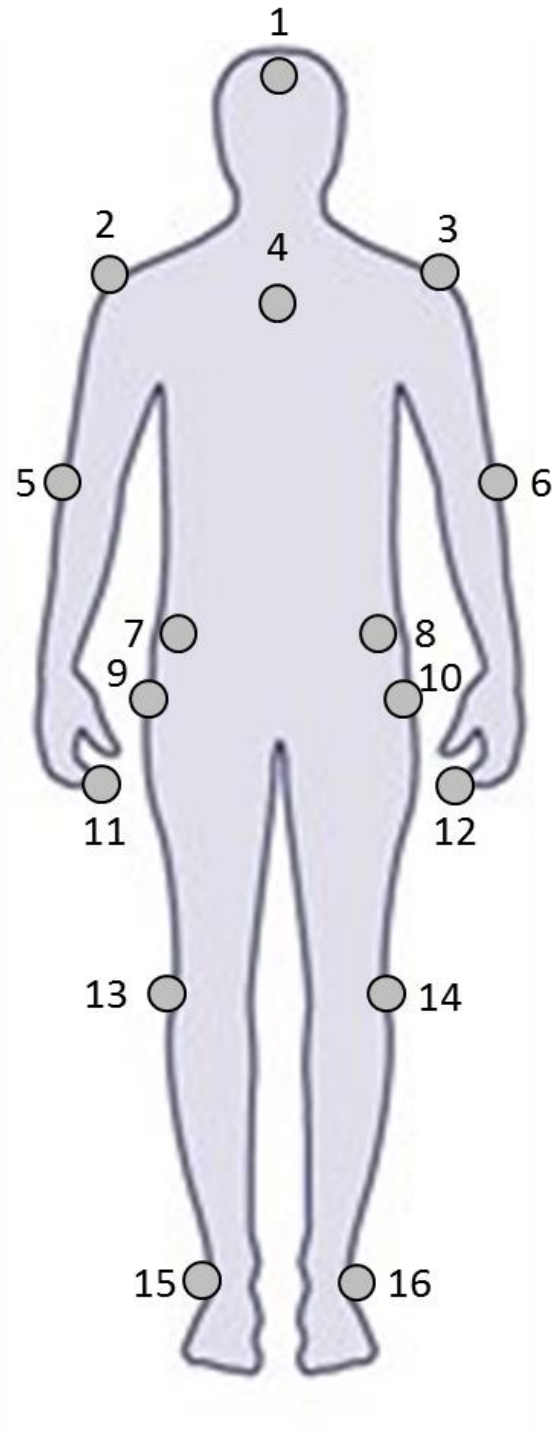

Figure 5.2: Reflective marker placement. Numbers correspond with exact anatomical landmarks defined In Table 5.1. Modified from hkadigital.co.uk.

Body Segment	Central Trajectory	Distal Trajectory	Planes of Analysis
Head	Right Acromion Process (2)	Forehead (1)	Transverse
Shoulders	Right Acromion Process (2)	Left Acromion Process (6)	Transverse
Pelvis	Right Anterior Superior Iliac Spine (7)	Left Anterior Superior Iliac Spine (8)	Transverse
Left Upper Arm	Left Acromion Process (3)	Left Olecranon Process (6)	Sagittal
Left Lower Arm	Left Olecranon Process (6)	Left Distal Third Phalanx (dorsal) (12)	Sagittal
Left Arm	Left Acromion Process (3)	Left Distal Third Phalanx (dorsal) (12)	Frontal
Left Upper Leg	Left Greater Trochanter (10)	Left Lateral Femoral Epicondyle (14)	Sagittal
Left Lower leg	Left Lateral Femoral Epicondyle (14)	Left Lateral Fibular Malleolus (16)	Sagittal
Left Leg	Left Greater Trochanter (10)	Left Lateral Fibular Malleolus (16)	Frontal
Right Upper Arm	Right Acromion Process (2)	Right Olecranon Process (5)	Sagittal
Right Lower Arm	Right Olecranon Process (5)	Right Distal Third Phalanx (dorsal) (11)	Sagittal
Right Arm	Right Acromion Process (2)	Right Distal Third Phalanx (dorsal) (11)	Frontal
Right Upper Leg	Right Greater Trochanter (9)	Right Lateral Femoral Epicondyle (13)	Sagittal
Right Lower Leg	Right Lateral Femoral Epicondyle (13)	Right Lateral Fibular Malleolus (15)	Sagittal
Right Leg	Right Greater Trochanter (9)	Right Lateral Fibular Malleolus(15)	Frontal

Table 5.1: Body segments (as defined by pairs of reflective markers) and the planes in which their movement was analysed. In each instance the movement analysed was that of the distal trajectory relative to the central trajectory. Numbers in parentheses correspond with marker numeration in Figure 5.2.

5.2.3 Protocol

Subjects walked on the pressure sensitive treadmill at a set speed of 1.1. m/s^{-1}. This speed was chosen as it was found to be comfortable for all subjects, all confirming that they felt secure walking at this speed. Both foot pressure and kinematics data were measured in two conditions: braced and non-braced. In the braced condition, subjects wore a lumbar brace: Double cross over lumbar brace (Physio-Med Services Ltd., Derbyshire, UK), and cervical brace: Adjustable cervical collar (Special Protectors Co., Ltd., Taiwan) in order to couple the trunk and pelvis; and head and shoulders, respectively (Figure 5.3).

Figure 5.3: Images of the cervical and lumbar braces used in the experiment. Braces were adjustable to fit all subjects accordingly.

In the non-braced control condition subjects walked freely and unrestricted as they would normally (within the constraints of the treadmill environment). Subjects first walked in the braced condition, and then after a short break the non-braced condition. For each condition, synchronous foot pressure and kinematic data were recorded in two consecutive 150 second periods, resulting in a total of five minutes' recording for each condition. If data collection was interrupted, for example if a reflective marker became detached

from the subject, or the subject's position on the treadmill drifted, the data were rejected and recording was repeated.

5.2.4 Data Analysis

Foot pressure records captured during both conditions were grouped into those made in the braced and non-braced conditions in each subject, and were then analysed and compared using an in-house technique, pedobarographic statistical parametric mapping (pSPM) (Pataky et al., 2008) (Appendices 1.1 – 1.3). Statistical parametric mapping, originally developed for analysis of functional magnetic resonance imaging (fMRI) scans (Friston, 1997), aligns each pressure record with all others in the data set so that structures optimally overlap, enabling comparisons to be made between them at the pixel level.

For kinematic analysis, each 150 second recording was imported into MATLAB (MathWorks, USA) and split into five 30 second sub-samples. This produced ten sub-samples, per condition, per subject. In each of these sub-samples, the minimum and maximum angle (Figure 5.4) for each segment in each plane of interest (as in Table 5.1, and represented diagrammatically in Figure 5.5) were calculated (Appendix A1.4). From these values a maximum range of excursion could then be calculated for each segment.

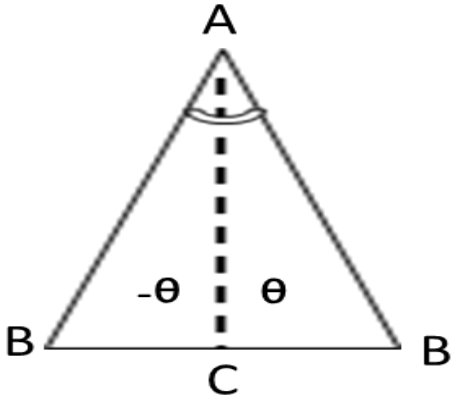

Figure 5.4: Angles (θ) calculated were those between a central trajectory (A) and a distal trajectory (B) as in Table 6.1. The angle measured is based on the intersection of vector A-B with the axis of interest (defined by A-C) hence the position of the distal trajectory B relative to that axis determined whether the angle was positive or negative

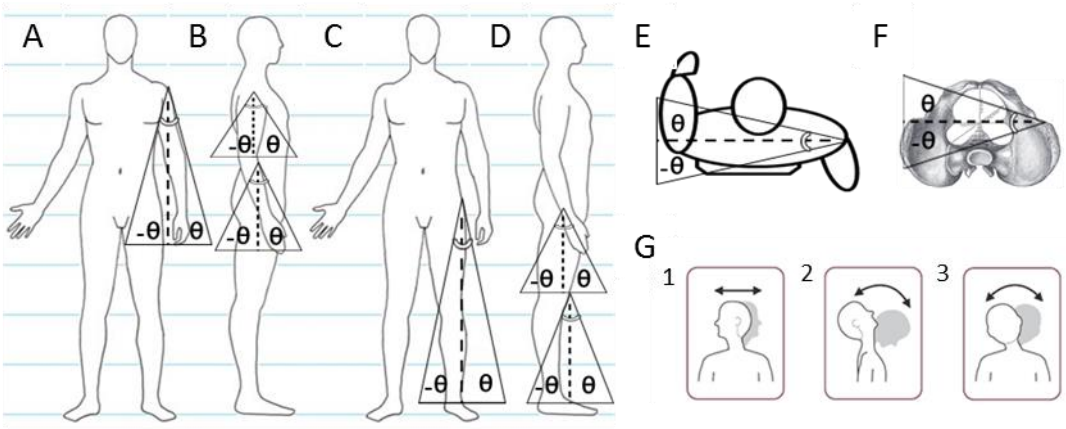

Figure 5.5: Diagrammatic representation of segment angles considered. This includes whole arm and leg abduction in the frontal plane (A and C respectively) and upper and lower arm and upper and lower leg swing in the sagittal plane (B and D respectively). Diagrams modified from medicalanatomy.net. E and F represent transverse plane analysis of shoulder and pelvic rotation respectively. Diagram F modified from bartleby.com/107/58. G represents head yaw(1), pitch(2), and roll(3) of which head movement was analysed with respect to the right shoulder. Diagram modified from resourcesonbalance.com. See Table 6.1 for exact anatomical landmarks.

On the whole kinematic capture was successful. In some subjects however, reflective markers were invisible to the camera system for considerable periods of time, and therefore if markers were captured for less than 80% of a 150 second recording, the resulting data were not considered to be fully representative. In these subjects, such markers were excluded from analysis, which in turn also led to the exclusion of certain body segments from the analysis. Through this exclusion, the following body segment angles were not calculated:

- Subject 4 (loss of left shoulder marker) - Shoulder rotation, Left upper-arm swing, Left arm abduction.
- Subject 10 (loss of left ASIS and greater trochanter markers) - Left lower-leg swing, pelvic rotation.

5.2.5 Statistical Analysis

All analysis was performed in MATLAB (MathWorks, USA) and SPSS (IBM, UK). To compare foot pressure records between groups statistically, mean square error was calculated for each foot-pressure record in each group

(braced and non-braced) and for each subject, in order to quantitatively define how each print differed from the mean (see Appendices A4.1-A4.10 for diagrammatic representations of foot pressure mean square error for each subject). The variance in mean square error for each group was then calculated and used as a measure of overall variability in foot pressure within the group. A repeated measures ANOVA was conducted following Bonferroni correction to assess whether differences in variance in mean square error were significant.

To determine under which regions of the foot that plantar pressure differed most, qualitative representations of plantar pressure distribution between the mean print and that with the highest mean square error were plotted.

Kinematic data-processing yielded ten maximum range of excursion angles for each segment angle, per condition (braced and non-braced) for each subject. From these ten angles, mean peak excursions and standard deviations were identified for each participant. Repeated measures ANOVA were conducted following Bonferonni correction to assess whether peak excursions for each body segment were significantly different across conditions.

5.3 Results

5.3.1 Foot pressures

Firstly, the effect of body segment recoupling on foot pressure variability was examined. This involved comparing foot pressure records during unrestricted treadmill walking (non-braced condition) with those made when neck and trunk motion were restricted with the body braces (braced condition). A repeated measures ANOVA determined that variance in foot pressure mean square error was significantly larger (F (1, 9) = 5.95, p = 0.04) during walking in the braced condition when compared to the unrestricted non-braced condition (8.63 ± 1.76 and 6.46 ± 1.53 respectively). (Figure 5.6).

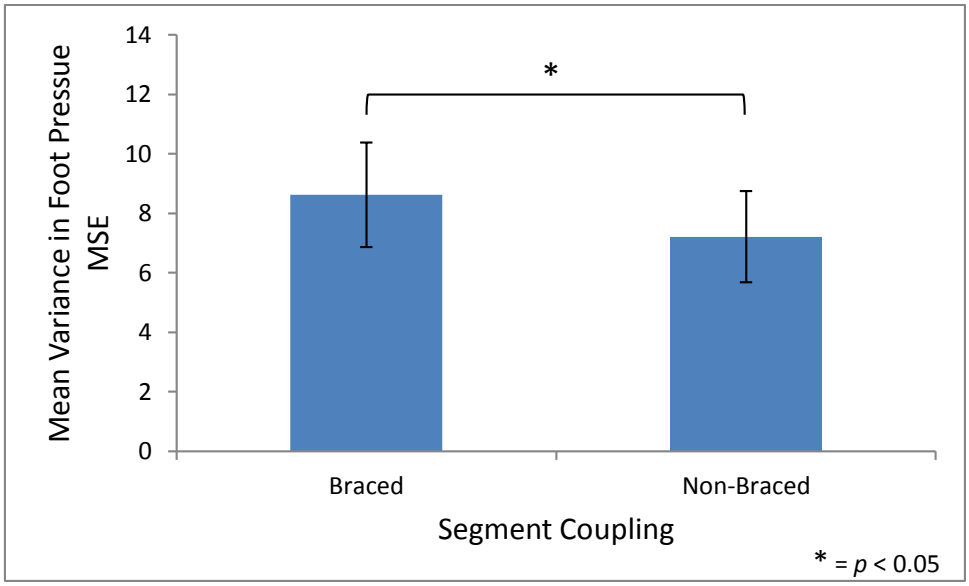

Figure 5.6: Comparison of variance in foot pressure MSE between Braced and Non-Braced conditions.

Despite the lack of significant difference in overall variance in foot pressure mean square error, a visual comparison of the mean foot pressure to the foot pressure record with the highest mean square error in each trial can still provide a qualitative impression of how foot pressure might vary with each condition in order to maintain balance (Figure 5.7). Figure 5.7 suggests that under-heel pressure remains relatively constant, but the differences expressed in the most variable pressure records are under the forefoot. These changes in underfoot pressure range through a more diffuse pressure across the lateral forefoot and midfoot (seen e.g. in subjects 1, 2, 6 and 8), and a shift in pressure under the medial forefoot and hallux (seen e.g. in subjects 4, 7 and 9) to a combination of both (subjects 3, 5, and 10).

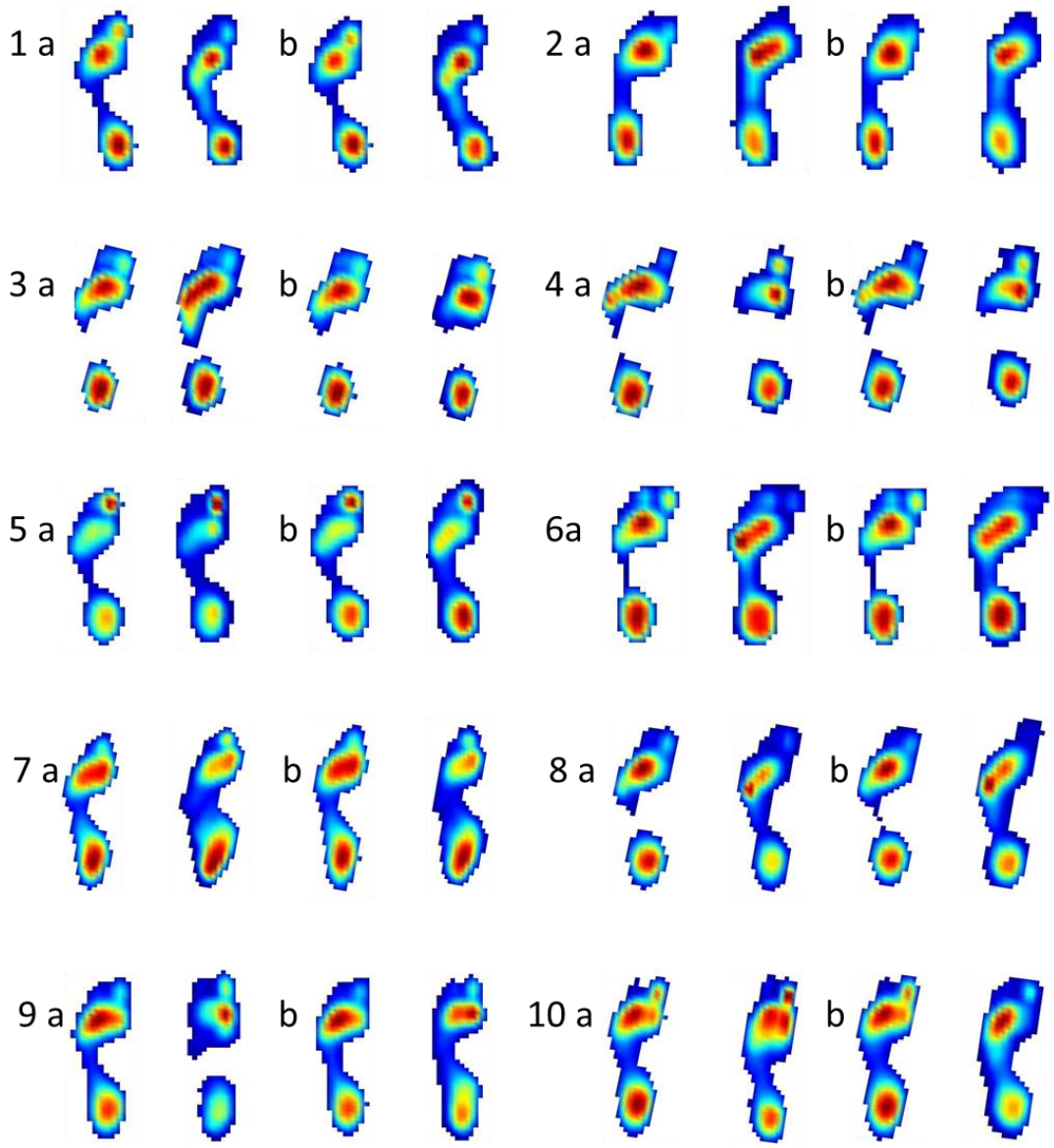

Figure 5.7: Visual comparison of foot pressure records for all subjects (1-10) in Non-Braced (a) and Braced (b) conditions. In each case the mean foot pressure record (left) is compared with the most varied foot pressure record (right).

5.3.2 Kinematics

Calculated body segment angles and the results of repeated measures ANOVAs are specified in Table 5.2. Within the upper body, significant differences in body segment range of excursions between the braced and non-braced conditions were observed in the head and the shoulders. The maximum

range of head pitch (°) was significantly lower (F (1, 8) = 6.51, p = 0.03) in the braced condition when compared to the non-braced condition (10.70 ± 0.78 and 14.69 ± 2.13 respectively). The maximum range of shoulder rotation (°) was also significantly reduced (F (1, 7) = 6.59, p = 0.04) in the braced condition (10.92 ± 0.91) when compared to the non-braced control (12.91 ± 0.92). No significant effect of gender, or interaction between bracing and gender, was observed for any of the upper body segments.

Within the lower body, significant differences in segment range of motion were observed only within the right thigh. In this case, the maximum range of right thigh swing (°) was significantly increased (F (1, 8) = 5.91, p = 0.04) in the braced condition (27.07 ± 0.25) relative to the non-braced condition (25.94 ± 0.49). There was also a significant effect of gender (F (1, 8) = 14.37, p = 0.01), with females demonstrating a larger range of right thigh swing than males (27.68 ± 0.44 and 25.33 ± 0.44 respectively). The effect of the interaction between bracing and gender on right thigh swing was, however, insignificant (F (1, 8) = 2.15, p = 0.18). No significant effect of gender, or interaction between bracing and gender, was observed for any other lower body segment.

Body Segment	Mean (°) Non-Braced Condition	Std. Error (°) Non-Braced Condition	Mean (°) Braced Condition	Std. Error (°) Braced condition	Mean (°) Female	Std. Error (°) Female	Mean (°) Male	Std. Error (°) Male	Repeated Measures ANOVA					
									Brace		Gender		Gender*Brace	
									F	*P*	*F*	*p*	*F*	*P*
Head Pitch	14.69	2.13	10.70	0.78	10.07	1.98	15.31	1.98	6.51	0.03	3.52	0.10	0.25	0.63
Head Roll	9.68	1.87	8.19	0.87	10.85	1.89	7.02	1.89	1.57	0.25	2.06	0.19	0.67	0.44
Head Yaw	18.12	1.47	17.16	1.48	18.02	2.21	17.26	2.21	0.57	0.47	0.06	0.82	0.00	0.97
Shoulder Rotation	12.91	0.92	10.92	0.91	12.21	1.15	11.23	1.28	6.56	0.04	0.32	0.59	1.85	0.22
Left Arm Abduction	12.13	2.10	11.83	1.58	7.44	0.69	7.42	0.72	0.10	0.77	0.00	0.98	1.18	0.31
Left Arm Swing	32.18	2.82	33.18	2.69	36.93	3.59	28.43	4.01	0.72	0.42	5.38	0.16	0.57	0.48
Left Bottom Arm Swing	55.75	3.36	55.21	3.31	61.92	4.79	49.04	4.79	0.11	0.75	3.62	0.09	0.00	1.00
Left Top Arm Swing	24.59	2.13	24.37	2.04	26.01	2.74	22.96	3.06	0.09	0.78	4.11	0.48	0.31	0.87
Right Arm Abduction	10.50	1.29	12.80	2.09	14.92	2.33	8.38	2.33	4.50	0.07	3.29	0.08	1.35	0.28
Right Arm Swing	26.69	2.32	28.13	2.35	27.32	3.22	27.50	3.22	1.98	0.20	4.56	0.97	2.98	0.12
Right Bottom Arm Swing	47.64	3.57	48.89	3.57	50.03	4.89	46.49	4.89	0.49	0.50	0.26	0.62	1.56	0.25
Right Top Arm Swing	21.28	1.46	21.66	2.13	24.24	2.47	18.70	2.47	0.12	0.74	2.52	0.15	2.25	0.17
Pelvis Rotation	10.86	0.67	10.43	1.21	11.97	1.16	9.32	1.30	0.22	0.65	2.33	0.17	0.18	0.68
Left Leg Abduction	7.00	0.22	7.86	0.92	7.44	0.69	7.42	0.77	1.02	0.35	0.00	0.98	0.10	0.76
Left Leg Swing	28.38	1.02	28.81	1.03	28.56	1.34	28.63	1.50	1.04	0.34	0.00	0.97	0.07	0.81
Left Thigh Swing	25.82	1.04	26.24	0.92	27.50	1.29	24.57	1.44	1.65	0.24	2.29	0.17	2.37	0.17
Left Shin Swing	55.43	1.57	55.27	1.56	56.04	2.20	54.66	2.20	0.34	0.57	0.20	0.67	0.33	0.58
Right Leg Abduction	7.21	0.44	6.95	0.50	6.48	0.66	7.68	0.66	1.94	0.20	1.67	0.23	3.89	0.08
Right Leg Swing	28.78	0.67	28.56	0.69	28.13	0.95	29.21	0.95	1.27	0.29	0.65	0.44	0.17	0.69
Right Thigh Swing	25.94	0.49	27.07	0.25	27.68	0.44	25.33	0.44	5.91	0.04	14.37	0.01	2.15	0.18
Right Shin Swing	56.82	1.07	56.36	1.22	58.29	1.61	54.89	1.61	2.50	0.15	2.23	0.17	0.01	0.91

Table 5.2: Results of kinematic analysis of body segment range of motion (°). Statistical results from repeated measures ANOVAs are reported

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5.4 Discussion

5.4.1 Foot pressures

Considering the impact of segment coupling on foot pressures, the results of this study support hypothesis (1), that foot pressures during the braced condition would become more variable when compared to unrestricted non-braced walking. It is suggested that this increased foot pressure variability reflects the actions of the lateral vestibulospinal reflex in controlling for impaired balance induced by the reduced efficiency of trunk counter-rotations. The resulting innervations of the extensor muscles of the legs may shift the centre of mass laterally in response to increased medio-lateral sway, leading to the resulting lateral pressure shift seen under the fore and midfoot as shown in Figure 5.7.

Further, such pressure distributions might also be expected during the 'lateral-ankle strategy' that modulates foot rollover, and which is the main balance strategy during single support (Hof et al., 2010, Hof et al., 2007, Hoogvliet et al., 1997). This strategy involves the contraction of muscles around the subtalar joint that induce a shift of the centre of the pressure under the foot and generate a stabilising moment of force to counteract unwanted body tilt (Hoogvliet et al., 1997). It is speculated that both actions may be of particular importance here, due to the restricted ability of the trunk to counteract the potentially destabilising torques produced by the swing leg (Ducroquet et al., 1968). Other muscle synergies, including those responsible for the hip strategy may also contribute to postural control through activity at the hip extensors (Shumway-Cook and Woollacott, 2000b). The restrictions placed on independent body segment rotations could therefore place increased demand on the vestibulospinal reflex and lateral ankle strategy to maintain balance, particularly during the single support phase.

5.4.2 Kinematics

5.4.2.1 Upper Body

The results partially upheld the hypothesis (2) that head and shoulder coupling would decrease head movement in all planes, with subjects demonstrating a significant decrease in mean peak excursion in head pitch during the braced condition.

Head stabilisation is a vital and complex component of locomotion, both from the perspective of gaze and postural control. This therefore requires delicate control in order to sample the surrounding visual environment and anticipate the need for obstacle avoidance, whilst maintaining the stabilisation of the head in space in order to provide a frame of reference or 'inertial guidance platform' (Mulavara et al., 2002).

During normal walking, the head is subjected to considerable pitch (Grossman et al., 1988). Indeed, both the vestibulopsinal and the vestibulocollic reflexes attempt to compensate for these movements in order to stabilise the head, thereby reducing the need for the vestibuloocular reflex to induce compensatory eye movements. It is therefore possible that the vestibulospinal reflex and vestibulocollic reflex were aided in this by the cervical brace, potentially explaining the reduced pitch observed. On the other hand, the fact that no significant effects were observed in head rotation and yaw may be an artifact of the restrictions of straight-line treadmill walking. That is, in the controlled, artificial conditions in which subjects were focusing on the task at hand, they had no real need to rotate the head to scan the visual environment. However, natural real-world locomotion clearly involves an array of dynamic movements, most importantly turns, which are known to initiate from the head (Grasso et al., 1998). This emphasises the need for further whole-body studies of this nature in (safely controlled) real world environments.

The hypothesis that (3) shoulder and pelvic excursions would be reduced in the braced condition was partially upheld. Whilst no significant effects of bracing on pelvic excursion were observed, subjects did

demonstrate reduced shoulder excursions when trunk counter-rotations were restricted. This suggests that accelerations from the swinging legs and pelvis are attenuated by the lumbar brace, and hence the reductions in shoulder accelerations observed support a passive arm swing hypothesis (Pontzer et al., 2009a).

The hypothesis (4) that trunk and pelvis coupling would alter arm swing and abduction in the braced condition was not upheld as no significant effects of bracing on arm swing or abduction were observed for either arm. However, it is suggested that an increase in *active* am swing in the braced condition is being masked due to the reduction of shoulder acceleration. In other words, the reduction in passive arm swing due to attenuated shoulder rotations evokes an increase in active arm swing, hence maintaining overall arm swing at the same level in order to preserve balance. This does have clear implications for energy expenditure however.

5.4.2.2 Lower Body

As mentioned above, pelvis excursion was not significantly different between the braced condition and non-braced control. It is therefore possible that active arm swing, as well as maintaining overall arm swing levels, is also therefore assisting with the active maintenance of pelvic excursion. Again however, the energetic cost of increased active arm swing would have an effect on the extent to which this strategy could be utilised, likely making it unsuitable for longer periods of activity. As this study had subjects walk in the braced condition for five minutes only, future studies may wish to consider the longer term implications of restricted counter-rotations on active control of the torso.

When considering leg swing, *contrary* to hypothesis (5) that leg swing would decrease in the braced condition, there actually appeared to be increase in upper leg excursion in the right leg in the braced condition. As it is highly likely that the restrictions on counter-rotations of the trunk and impacted upon forward propulsion, it is possible that the increase in right upper–leg excursion seen in the braced condition indicates a compensating role of the hip extensors (Sadeghi et al., 2001b, Riley et al., 2001) in order to

maintain forward propulsion. As studies suggest that the left leg is usually dominant for postural stabilisation, and the right for mobilisation (Hirokawa, 1989), the lack of significant differences in the left leg suggests that propulsion is affected more than balance, with reduced the effects of bracing appearing to be well compensated for. The significant increase in right thigh swing in females when compared to male also partially upheld the hypothesis that (6) gender differences in segment kinematics would be observed. Indeed, this again likely reflects a need for greater action of the hip extensors in females to maintain propulsion and step length due to the typically shorter leg length.

No consistent effects were observed with regards to leg abduction in either leg, suggesting that subjects did not increase their step width during the braced condition in an attempt to increase their base of support. This may therefore imply that the increase in active arm swing, as discussed above, is a more efficient and effective method for aiding with the control of balance.

5.4.3 Societal and Clinical Implications

Although the compensatory mechanisms that have been observed in young subjects serve to support balance when counter-rotations of body segments are restricted, there are clear implications for those with motor coordination deficits, including the elderly. Among contributing intrinsic factors is reduced joint mobility: in part due to mechanical deterioration, both at the joint surfaces and in muscle, tendon and ligaments; alongside numerical loss of muscle fibres and loss of muscle strength (Freemont and Hoyland, 2007). As a result, reduced rotational freedom of the head, trunk, and pelvis, interferes with both counter-rotations required to maintain stability, and the redirection of gaze (Chiacchiero et al., 2010, Cinelli et al., 2008, Paquette et al., 2006, Van Emmerik et al., 2005). Loss of spinal stability also leads to decreased range of spinal rotation, as observed during standing-reach tasks and when twisting when sitting (Cavanaugh et al., 1999, Schenkman et al., 1996).

Furthermore, when compared to the healthy elderly, those with Parkinson's disease are subject to several changes in motor patterns that further increase the risk of gait disturbance. It has long been known that the coordination of multiple motor components poses a challenge in Parkinson's disease (Benecke et al., 1986). Typically, the head and trunk move en bloc (Vaugoyeou et al., 2006) and pelvic rotation has been found to be limited (Vallabhajosula et al., 2012), possibly indicating inability in uncoupling shoulder and pelvic segments to produce effective trunk rotations. Axial rotations are also smaller and slower compared to healthy older adults (Vallabhajosula et al., 2012), which is a likely consequence of disease-related rigidity and bradykinesia and the resulting lesser and slower muscle response (Halliday et al., 1998).

As these results demonstrate gait changes in response to 'en bloc' movements of body segments even in healthy, young individuals, it is highly likely that any effects observed in the elderly and infirm could be further exacerbated, by influences including reduced muscle strength, and increased joint stiffness, as discussed above. For instance, the potential impact of restricted head movements during dynamic movements such as turning has already been discussed. Turning is known to be particularly difficult and pose a significant threat to balance in the elderly, with around 30% of falls in occurring during a turning movement or when bending (Patla et al., 1992). These falls are particularly debilitating, as they often result in hip fracture, with a fall during turning almost eight times more likely to cause fracture than a fall when walking straight (Cumming and Klineberg, 1994).

As the sequential top-down control of body segments has proved to be of major importance in turning initiation, it is fair to assume that the restrictions placed on this sequential activation of body segments through reduced shoulder accelerations and more 'en bloc' movements of body segments could be a significant factor in turning inefficiency in these individuals. Indeed, the elderly often employ more energetically costly and destabilising spin turns (Akram et al., 2010), in which a change in direction is achieved by spinning around on the supporting leg (Hase and Stein, 1999).

The results also suggested that increased active arm swing could be of particular importance in providing counter-torsional forces when the trunk is restricted. Conversely, it has been shown that arm swing speed and amplitude are often reduced in the elderly (Elble et al., 1991), perhaps through over-caution, and that this is further exacerbated in elderly fallers (Wolfson et al., 1990). Consequently, reducing arm swing appears to be counter-productive, and this could therefore emphasise the potential for training interventions in such individuals.

The increased activity in the upper leg observed as a response to segment coupling may also have implications in the elderly. The importance of the hip extensors in control of balance in the elderly has been documented (Sadeghi et al., 2001a), and indeed, if the increased upper leg excursion observed reflects an increase in activity at the hip joint, this adaptation to increased trunk stiffness may well contribute to increased risk of femoral fracture in the elderly, a major cause of mortality and disability (Kanis and McCloskey, 1996).

5.4.4 Evolutionary implications

The results of this study could also have a number of implications when considering the bipedal gait of early hominin species, particularly *Australopithecus afarensis,* in which a funnel-shaped thorax and lack of a full waist (Schmid, 1989, Schmid, 1991, Berge, 1994); and the extensive muscular connections between the head and shoulders (Stern Jr and Susman, 1983), have traditionally been considered characteristic. The mosaic of features observed in the species has led to the gait of *Australopithecus afarensis* becoming the subject of considerable debate. Historically, fossil evidence of retained adaptations to arboreal locomotion ((Stern Jr, 2000, Stern Jr and Susman, 1983, McHenry and Berger, 1998) led some researchers to argue that it would have been unlikely and inefficient for *Australopithecus afarensis* to walk fully erect as in modern man

(Stern Jr, 2000, Berge, 1994, Duncan et al., 1994, Berge, 1991, Ruff, 1988, Berge and Kazmierczak, 1986, Berge, 1984, Stern Jr and Susman, 1983).

However, others suggest that the gait of *Australopithecus afarensis* would in fact have been more like our own (Crompton et al., 1998, Latimer, 1991, Latimer and Lovejoy, 1989, Lovejoy, 1988, Latimer et al., 1987, Latimer, 1983) and through advantages in computer modelling techniques, the case for a fully erect *Australopithecus afarensis* has become much stronger (Sellers et al., 2005). Indeed, this is supported by the recent reconsideration of mounting fossil evidence suggesting that most of the perceived differences in segment proportions between *Australopithecus* and *Homo* can simply be attributed to differences in body size (Antón, 2012, Holliday, 2012, Pontzer, 2012). Therefore, although caution must be exercised when applying the results of this study, they could provide useful insights into our evolutionary history.

Interestingly, the lack of any definitive changes to head rotations by the recoupling of the head and shoulders could imply that the extensive muscular connections between the head and shoulders in *Australopithecus afarensis* may not have restricted rotational movements to a significant degree when compared to later hominins and ourselves. Although, as discussed, this also needs to be assessed in dynamic movements such as turns, in which rotational movements of the head are known to be critical. In fact, these results suggest that the coupling of the head and shoulders may have actually been of benefit in reducing unwanted head tilt. In turn, this may emphasise the importance of the extensive neck muscles in the species in holding the head upright, particularly because of the position of the foramen magnum. Indeed, it has been shown that the primitive vestibular system of *Australopithecus* would be unable to compensate for large scale head movements (Spoor et al., 1994), and it is therefore likely that large scale head rotations were of relative unimportance in the species.

In contrast, the putative (Bramble and Liebermann, 2004) persistence hunting, endurance runner *Homo erectus* demonstrates both a more complex vestibular system (Spoor et al., 1994), and greatly reduced

muscular connections between the head and neck (Aiello and Dean, 1990), which might suggest that greater independence of the head and pectoral girdle only became important when our ancestors began to track and hunt moving prey (Bramble and Lieberman, 2004).

The results of this study also confirmed the hypothesis that trunk and pelvis coupling would reduce shoulder movements. Therefore it is fair to assume that the funnel-shaped thorax of *Australopithecus afarensis* would most likely have resulted in smaller shoulder rotations, thereby reducing the efficiency of counter-rotations. The results also demonstrated that, as a consequence, active arm swing may be of particular importance in balancing angular momentum when the movement of the trunk is restricted. Interestingly, the upper-limb morphology of *Australopithecus afarensis* lends itself to efficient arm swing, with an intermembral index (IMI) of roughly 88 (Wang et al., 2003, Johanson et al., 1982, Jungers, 1982) compared to 68-70 in modern man (Wang et al., 2003). IMI is a ratio comparing upper and lower-limb length, with an index of 100 representing exactly equal length. When the upper and lower limb are the same length, the phasing between them is also equal and hence energetic efficiency is optimal (Wang et al., 2003, Witte et al., 1991). Thus, the larger moment of inertia generated by the longer upper-limb, and the greater efficiency of matching the swinging frequency with the lower limb, would have made the generation of counter-torsional forces more efficient in *Australopithecus afarensis* when compared to modern man. These features would therefore prove of particular benefit in balancing angular momentum, and may help to explain how the species would have been likely to walk fully erect at a lower cost than walking bent-hip, bent-knee (Sellers et al., 2005) despite the restrictions placed upon shoulder rotations.

The gender-based differences observed in upper leg excursions also point to possible gender differences in gait patterns in *Australopithecus afarensis.* Indeed, there is considerable evidence to suggest that the species was sexually dimorphic, although there is debate as to whether this was to a similar level as in modern humans (Reno et al., 2010, Reno et al., 2003) or to

a much larger degree (Richmond and Jungers, 1995, McHenry, 1991, Stern Jr and Susman, 1983). It is possible therefore that gender differences in gait could have been further exaggerated in the species. As of yet, most biomechanical models of, and discussions surrounding the gait of, *Australopithecus afarensis* are based on the female skeleton 'Lucy', AL 288-1, as the most complete specimen. However, this specimen is at the low end of the range for body size in this species and hence segment proportions may be atypical of the species (see discussion above). These results therefore highlight the need to consider interspecific morphological variation, including sex-differences.

5.4.5 Conclusion

This study set out to examine the effects of body segment coupling on foot pressure variability and kinematics in young healthy subjects. It has demonstrated that coupling of the head and shoulders, and of the trunk and waist, reduces peak shoulder rotations and hence is likely to have reduced the efficiency of counter-rotations of the trunk necessary to balance the centre of mass.

These changes in upper body rotational efficiency appeared to be compensated for in leg swing. Both male and female subjects exhibited the same changes in leg swing during segment coupling, with increased upper leg swing a potential strategy maintaining forward propulsion, however this appeared to be increased in females, possibly due to shorter leg length. Conversely, arm swing and abduction did not appear to be effected, but the possibility that increased active arm swing during segment recoupling acts to maintain arm swing to the same level has been discussed.

Perhaps surprisingly, the effect of head and shoulder coupling on head rotations appears to be insignificant, with only head pitch appearing to be reduced. However, this may be an artifact of straight line walking, and further study is needed to assess how reduced head rotations may impact on dynamic movements such as turning.

The results of this study may have considerable implications for the elderly, in whom joint stiffness and declines in muscular strength may

contribute significantly to reduced counter-rotations of body segments. Indeed, the changes to leg swing observed appeared to reflect the strategies seen in the elderly, including reduced step length and increased activity of the hip extensors. However, the differences observed in arm swing strategy imply that reduced arm swing through over-caution in the elderly may be counter-productive, and hence highlight the potential benefits of training and exercise interventions in such individuals.

Further, these results may also provide insight into our evolutionary history, particularly with respect to *Australopithecus afarensis*, a species known to be bipedal but characterised by a coupled head and shoulders, and coupled trunk and pelvis. These results may highlight the importance of the relatively long arms of *Australopithecus afarensis* in maintaining sufficient counter-rotations of the funnel-shaped thorax.

Chapter 6: Overall Conclusion

6.1 Project Summary

Using what is to date a uniquely whole-body, multimodal approach, this thesis has assessed the potential impact of sensory load and the decoupling of body segments on foot pressure variability and hence stability. This assessment was accomplished using a combination of foot pressure analysis, motion capture and kinematic analysis of body segment movements, and eye tracking analysis.

The project aimed to answer the following research question:

'How might increased sensory demand, and the recoupling of body segments in modern humans impact on foot pressure variability during walking, and what are the implications for human evolution, and for modern humans with respect to ageing and the increasing complexity of built environments?'

From this question, two overarching hypotheses were developed:

1) **Sensory prioritisation during walking will result in decreased efficiency of postural control as it acquiesces to support the processing of visual and auditory stimuli of varying complexity.**

2) **The recoupling of the head and neck, and trunk and pelvis will result in changes to postural control as a consequence of the reduced effectiveness of the counteraction of destabilising torques through trunk counter-rotations.**

6.2 Summary of Experimental Conclusions

Chapter 3 presented the results of a study assessing how foot pressure variability was affected by visual object tracking against varying levels of visual clutter. This involved the comparison of foot pressure records made during gaze fixation of a static object with those made during Smooth Pursuit against backgrounds of varying complexity. The results of this study demonstrated that in young healthy subjects, eye movement and visual tracking complexity does not significantly impact on foot pressure variability and hence stability when walking. It is likely that this reflects a high degree of adaptation to tracking moving stimuli, including predator or prey animals, in our evolutionary history. However, postural control was seen to be affected by the level of background visual clutter, with increased variability in foot pressures seen when tracking against a blank background. It is suggested that this is a consequence of the lack of static referents to which posture can be coupled, and from which information about target position and speed can be deduced.

Chapter 4 extended the object tracking task considered in Chapter 3 by incorporating a dual visual-auditory task. This enabled the comparison of the impact of filterable background auditory stimuli with a repeat-back language task requiring an active response, and the potential effects of processing prioritisation on foot pressure variability. It was concluded that the significantly increased foot pressure variability observed during the repeat back language task was the result of high demand on shared neural circuits, particularly those requiring the planning and execution of motor acts such as those in the frontal lobe. This leads to the acquiescence of postural control as visual and auditory input take priority. Interestingly, the lack of significant differences in foot pressure variability when the repeat-back language task was made more difficult with the addition of the more complex forest background, indicates that a ‘ceiling’ may be present at which sensory load ceases to impact on postural control. This was also supported by the lack of significant difference in foot pressure variability between subjects trained in gymnastics with those not trained in hand eye coordination-centred sports.

Finally, Chapter 5 considered the effects of the restriction of independent counter-rotations of body segments on whole body kinematics, and foot pressure variability, through the use of medical body braces. It was concluded that coupling of the head and shoulders, and of the trunk and waist, reduces peak shoulder rotations and hence is likely to reduce the efficiency of counter-rotations of the trunk necessary to balance the centre of mass. The potential need for increased active arm swing as a consequence was discussed. Changes in leg swing during segment coupling were also seen, with increased upper leg swing appears to act as a strategy to maintain forward propulsion. The larger upper leg excursions seen in females may reflect a larger need for this hip extensor activity due to typically shorter leg length. It was also concluded that the lack of an effect of segment coupling on head rotations (roll and yaw) may be an artifact of straight line walking, and further study is needed to assess how reduced head rotations may impact on other dynamic movements. Finally, foot pressure variability was shown to be increased when segments were coupled, indicating an increased need for postural control.

6.3 Conclusions about the Research Question

As noted above, this project set out with the following research question in mind:

'How might increased sensory demand and the recoupling of body segments in modern humans impact on postural control, and what are the implications with respect to the built environment, ageing, and the evolution of human postural control?'

The conclusions of Chapters 3 and 4 suggest that foot pressure variability does indeed increase with the difficulty of both visual and auditory tasks, supporting the first overarching hypothesis of this thesis, that: '**Sensory prioritisation during walking will result in alterations to postural control as attention is allocated to secondary tasks of varying complexity'.**

The second overarching hypothesis stipulated that: '**The recoupling of the head and neck, and trunk and pelvis, will result in alterations to postural control as a consequence of the increased rigidity of the thorax segments'.**

This hypothesis is upheld by the conclusions made in Chapter 5 concerning the increased variability in foot pressures with restriction of the head and pelvis movements. They further show the compensatory changes to leg swing, although these changes were subject to gender differences.

Therefore, it is concluded that both increasing sensory demand, and the recoupling of body segments have a clear impact on foot pressure variability as the body attempts to maintain stability. However the results suggest that a baseline level of visual stimulation is necessary as a referent against which to determine the position of the body in space, and equally that a ceiling effect may also be present beyond which no further impact on postural control is observed.

6.4 Implications

6.4.1 Evolutionary implications

The clear benefit of reduced sensory load to stability during walking demonstrated in Chapters 3 and 4 suggests that the consequent optimisation of neuroprocessing abilities resulting from a spread of hominins into more open grassland and savannah environments (albeit that *Homo erectus* also reinvaded tropical rainforest environments in South East Asia very quickly, see e.g. Elton, 2008) may have aided/been exaptive for the evolution of new cognitive behaviours, such as tool use, in late australopiths. Thus, it may further help to explain why hominins that had yet to benefit from the large increase in brain size and encephalization seen in *Homo* from 500 Ka onwards (see e.g. Antón, 2003), were able to develop cultural style in tool manufacture: clearly evinced in Acheulean industries from as much as 1.76 Ma (Lepre et al., 2011).

Further, the putative persistence hunting lifestyle of *Homo ergaster* and *Homo erectus* (Bramble and Lieberman, 2004, Carrier et al., 1984), and

the resulting importance of stability whilst tracking and hunting moving prey efficiently, is a key example, in our evolutionary history, of selective pressures which might be exerted by tasks generating large cognitive load. Persistence hunting is likely to have placed significant selective pressures on the efficiency of visuo-motor integration, and hence the ability to process sensory input and consequent motor tasks simultaneously, further optimising for cognitive processing capabilities, especially in dual-task scenarios. The increased foot pressure variability with dual tasking that is evinced and discussed in Chapter 4, although in itself not demonstrating any connection to human evolutionary history, implies that the development and perfecting of the persistence hunting lifestyle, alongside the development of other cognitively demanding dual-tasking processes such as the development of speech, wider social intercourse and tool use, are likely to have posed a threat to balance control. As such, the honing of these abilities may have played a significant role in the optimisation of multi-modal integration to ensure optimal bipedal efficiency.

Alongside sensory adaptations, the results discussed in Chapter 5 indicate that the efficiency of bipedal gaits is likely to have been significantly improved in *Homo* as a result of acquisition of independent rotations of the head and shoulders, and trunk and pelvis. The reduced foot pressure variability in natural walking in modern humans, when compared to the braced condition, surely reflects a reduced need for corrective postural control. Further, the gender differences in leg swing observed indicates the importance of exercising caution when proposing locomotor strategies for hominin ancestors based solely on fossil evidence, particularly due to an added need to consider the high degree of sexual dimorphism known in species such as *Australopithecus afarensis.*

6.4.2 Implications for Ageing and the Built Environment

Alongside the evolutionary implications, the results of each of the studies are of course highly relevant when considering safety in the typically complex environments prevalent in modern society. The observed impact on foot pressure variability of high levels of visual and auditory stimuli in young,

healthy subjects that is discussed in Chapters 3 and 4 has clear implications for the elderly and infirm. Reduced visual function with ageing is known to alter eye movement control (Knox et al., 2005, Spooner et al., 1980, Sharpe and Sylvester, 1978), and has been directly linked to the incidence of falls (Abdelhafiz and Austin, 2003, Ivers et al., 2000, Grisso et al., 1991). It is well known that the elderly have trouble allocating attention to additional tasks (Shumway-Cook and Woollacott, 2000a, Teasdale et al., 1991), making multi-modal integration, and hence the control of postural stability increasingly difficult. It is therefore likely that the effect of dual tasking would exacerbate the effects on postural control that have been described here for young, healthy subjects, in which integration is optimal.

The above considerations therefore prompt careful consideration of the complexity of sensory stimuli during the design of built environments, so as to optimise both safety and usability, particularly with respect to vulnerable users. Examples of environments which may be of particular concern include pedestrian crossings, and areas with high pedestrian turnover including shopping centres and train stations. This research highlights the importance of providing adequate visual referents in the visual field from which to determine information regarding body position. This consideration supports previous work showing the positive effect of appropriately positioned perceptual anchors on the reduction of body sway in the presence of complex environments (Meyer et al., 2012, Meyer et al., 2013), which are likely to be of similar or possibly even greater benefit to postural control during dynamic movements.

The results of Chapter 5 also offer insight into the '*en bloc*' movements of body segments typical of the elderly. The results of the segment recoupling study in young, healthy subjects suggested that increased active arm swing could be of particular importance in providing counter-torsional forces when the trunk is restricted. Conversely, it has been shown that arm swing speed and amplitude are often reduced in the elderly (Elble et al., 1991), and this could therefore emphasise the potential for training interventions in such individuals.

The increased activity in the upper leg observed as a response to segment coupling may also have implications in the elderly. The importance of the hip extensors in control of balance in the elderly has been documented (Sadeghi et al., 2001a), and their increased activity could contribute to increased risk of femoral fracture in the elderly, a major cause of mortality and disability (Kanis and McCloskey, 1996).

6.5 Limitations and Further Research

Despite the contribution of these conclusions and their implications to both evolutionary history and modern man, this project has nonetheless been subject to limitations. For instance, the very nature of treadmill walking is expected to have an effect on the rhythm of gait, which may in turn produce bias in the foot pressure data. Further, it is of course restricted to straight-line walking. Evidence suggests that dynamic movements, particularly turning movements, are more highly correlated with fall risk, and hence it would be expected that the effects on foot pressure variability observed would be further exacerbated when walking in more variable paths and especially in turning.

Furthermore, as a consequence of the large volume of data engendered by this study and the resulting time constraints imposed by required processing time, the degree of pupil movement within the visual and dual task trials was not able to be analysed as part of this project. As eye movements have been shown to initiate turning movements (Grasso et al., 1998), it is of clear importance to consider the impact of pupil movements on dynamic movements.

Due to lack of appropriate lab facilities to allow the pursuit of ethical permission, it was also not possible to conduct trials on elderly subjects, for which these results have important implications, as discussed extensively above. Consequent to the well-documented changes in walking patterns in such subjects, arising from both visual and motor decline and over-caution, unfortunately these results can only go so far in indicating how the elderly may be affected by visual and auditory clutter.

Further research should therefore extend similar studies to the elderly - and the infirm, such as those with Parkinson's disease - as these subjects could particularly benefit from increased knowledge of sensorimotor integration during complex tasks. To remove the bias induced by artificial environments and treadmill walking, real world data should be collected wherever possible. This would also allow for the consideration of dynamic movements. The analysis of pupil movement data would complete a whole-body picture of the motor response to sensory stimuli.

6.6 Closing Statement

This thesis aimed to assess the impact of sensory load and body segment coupling during walking, with implications for both human evolution and modern ageing in built environments. It has provided a unique contribution to our understanding of how sensory load and segment decoupling may have contributed to the success of our persistence hunting ancestors through the use of human analogues, the results of which are also directly relevant to the elderly in which sensory processing, motor control, and joint stiffness are of particular concern.

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8 Appendices

Appendix 1: Supplementary Information for Materials and Methods

```
% Function to read in data from EyeTrac and plot the V or H pos
values to
% permit sectioning of data based on eye movement and return timing
% information. Input data should be exported text files from Eye
Tracker
% software with the header removed. Also enter X or Y for H or V
movements

function eyeTracker(infile,xy,cuts)

global CUTPOINTS;
CUTPOINTS=zeros(cuts,1);

[X,Y]=loadEyeData(infile);                              % Read data
from file

if xy=='X'
    plot(X);
else
    plot(Y);
end
%set(gca,'XLimMode','manual','YLimMode','manual');  % Fix axes
limits
set(gcf,'numberTitle','off','name','eyeTracker')
set(gcf,'menubar','none','closeRequestFcn',@closeFigure)
hold on;

for i=1:cuts;
    [x,y] = ginput(1);  % Select a point with the mouse
    x = round(x);       % Round x to nearest integer value
    plot([x x],get(gca,'YLim'),'k--');  % Plot dashed line

    CUTPOINTS(i)=x;

end

assignin('base','CutPoints',CUTPOINTS)
hold off
delete(gcf)



function[X,Y]=loadEyeData(infile)

[A,D]=importdata(infile);
AA=A.data;

[a,b]=size(AA);

for i=1:a
    if AA(i,6)==0
        start=i;
        stime=AA(i,1);
    end
end
```

```
j=1;

for i=start:a
    ctime=AA(i,1);
    if (ctime-stime)<300
        X(j)=AA(i,2);
        Y(j)=AA(i,3);
    end
    j=j+1;
end

function closeFigure(varargin)
%%%%%%%%%%%%%%%%%%%%%%%%%
global CUTPOINTS;
assignin('base','XY',CUTPOINTS)
hold off
delete(gcf)

%return
```

Appendix A1.1: MATLAB script to read in pupil position data from Eye-Trac system and plot the horizontal or vertical movement as a line graph. Sections of different eye movements are defined by plotting crosshairs along the graph and the timing information (frame number) for each is then returned. These values can then be correlated with frame numbers from the treadmill data output and the prints made during each section/type of eye movement grouped together.

```
% Function to extract Eye XY positions from Viewpoint Eyetracker
%
% Syntax: EyeData=getEyeData(infileName, Axis);

function[A,B,timing]=getEyeData(infile, XY)

fprintf('\nWarning! This code is intended for use with ViewPoint
EyeTracker\n\n');
fprintf('The following assumptions are made with respect to the
data:\n');
fprintf('%c1. The Auto Calibration option was used\n',9);
fprintf('%c2. The system was opperating in Binocular mode\n',9);
fprintf('%c3. The Start/Stop control was via external
triggering\n',9);
fprintf('%c4. No Event data was written to the output file\n',9);
fprintf('%c5. The input file name is valid for a file in the current
directory\n',9);
fprintf('%c6. The full file name including extention is entered e.g.
''Trial_1.txt''\n\n',9);
fprintf('If any errors occure during data extraction the most likely
cause is\n');
fprintf('a corrupted data file or incorrect setting/aquisition
options where used.\n\n');

inp=fopen(infile,'r');

% Scan over header
tag=0;
while tag ~= 16
    tag=fscanf(inp,'%d');
    if tag~= 16
```

```
        fgetl(inp);
    end
end

% Check correct positioning in file
tline=fgetl(inp);
if strcmp(tline,'.000000    STARTUP.BMP')~=1
    fprintf('\n\nERROR! Cannot find start of data block\n\n');
    A=-1;
    B=-1;
    return
end

% read in eye data
line=1;
while ~feof(inp)
    tline=fgetl(inp);
    a=sscanf(tline,'%d %f %f %f %f %f %f %d %f %f %d %f %f %f %f %f
%f %f %d %f %f %d %f %d');

    if a(1)==10
        eyeData(line,1)=a(2);
        eyeData(line,2)=a(4);
        eyeData(line,3)=a(5);
        eyeData(line,4)=a(15);
        eyeData(line,5)=a(16);
        line=line+1;
    end
end

[A,B]=despike(eyeData,XY);
timing=eyeData(:,1);
fclose(inp);
```

Appendix A1.2: MATLAB code for reading data from ViewPoint files where A is the returned movement for eye A in the axis specified by Axis. B is the same data for eye B. T is the timing data for the eye movement. Inputdata is the file name. Axis indicates which movement axis to use e.g. [A,B,T]=getEyeData('Subject1_Slide1_a.txt', 'X') will read in horizontal pupil position. A figure is displayed with two graphs, the top graph is the raw data and the bottom is the filtered result. The pupil movement profile can then be filtered to allow accurate positioning of transition points. Whilst excessive filtering is not normally recommended, as eye movement data was not analysed this was not a concern.

```
% Function to permit sectioning of data based on eye movement and
return timing
% information. Input data should be exported text files from Eye
Tracker
% software with the header removed. Also enter X or Y for H or V
movements

function eyeTracker(A,B,t,cuts)

global CUTPOINTS;
CUTPOINTS=zeros(cuts,1);

plot(t,A,'DisplayName','A','XDataSource','t','YDataSource','A');hold
all;plot(t,B,'DisplayName','B','XDataSource','t','YDataSource','B');
hold off;figure(gcf);
```

```
legend('EyeA','EyeB');

set(gcf,'numberTitle','off','name','eyeTracker')
set(gcf,'menubar','none','closeRequestFcn',@closeFigure)
hold on;

for i=1:cuts;
    [x,y] = ginput(1);  % Select a point with the mouse
    x = round(x);       % Round x to nearest integer value
    plot([x-2 x-2],get(gca,'YLim'),'k--');  % Plot dashed line
    plot([x+2 x+2],get(gca,'YLim'),'k--');  % Plot dashed line

    CUTPOINTS(i)=x;

end

assignin('base','CutPoints',CUTPOINTS)
hold off
delete(gcf)


function closeFigure(varargin)
%%%%%%%%%%%%%%%%%%%%%%%%%%
global CUTPOINTS;
assignin('base','XY',CUTPOINTS)
hold off
delete(gcf)

%return
```

Appendix A1.3: MATLAB script to superimpose pupil movement profiles from both eyes on to a line graph on to which crosshairs can be plotted to select transition periods between types of eye movement. The program then returns a variable called CutPoints containing the timing information for the cuts.

```
function Zebris_NoGUI(varargin)

% check for existance of input struct
if exist('ZebStruct.mat','file')
    load('ZebStruct');
else
    disp('Error: ZebStruct.mat not found!');
    return
end
if exist('ZebStruct','var')==0
    disp('Error: ZebStruct variable not found!');
    return
end

% check that specified input file exists
if exist(ZebStruct.InFile,'file')
    infile=ZebStruct.InFile;
else
    a=sprintf('Error: Input file %s not found',ZebStruct.InFile);
    disp(a);
    return
end
```

```
% get print count L and R and number of frames and rate:
% these are stored in proc_info.mat

%[Lcount,Rcount,Fcount]=getPrintCount(infile);
getPrintCount(infile);

% extract prints
extractPrints(ZebStruct);

% check if option to skip registration selected

stcmp=strcmp(varargin(1),'noReg');
if stcmp
    fprintf('\nNo Registration Selected\n');
    return
end

% register prints

res_name2='Zeb_Batch';
save res_file_name res_name2;
if ZebStruct.RegPeak
    PP=dir('??_P*.mat');
    p=size(PP);
    if p(1)==0
        disp('Error: No Peak Pressure Prints');
        return
    end
    if ZebStruct.RecLandR
        zebris_regallLandR(PP); % if L & R seperate
    end
    if ZebStruct.RecLtoR
        zebris_regallLtoR(PP);  % if L flip to R
    end
    if ZebStruct.RecRtoL
        zebris_regallRtoL(PP);  % if R flip to L
    end
end

if ZebStruct.RegImpulse
    IP=dir('??_I*.mat');
    i=size(IP);
    if i(1)==0
        disp('Error: No Impulse Prints');
        return
    end
    if ZebStruct.RecLandR
        zebris_regallLandR(IP); % if L & R seperate
    end
    if ZebStruct.RecLtoR
        zebris_regallLtoR(IP);  % if L flip to R
    end
    if ZebStruct.RecRtoL
        zebris_regallRtoL(IP);  % if R flip to L
    end

end
```

```
system('del proc_info.mat');
system('del Pinfo.txt');
system('del res_file_name.mat');

% Function to count number of prints in input file
% No error checking, assumes that input file is correct format. If
not
% then will fail

%function[Lc,Rc,count]=getPrintCount(infile)
function getPrintCount(infile)

inp=fopen(infile,'r');

% read past header and get count
for i=1:14
    tline=fgetl(inp);
end
[a,b]=strtok(tline);
rate=str2double(b);
tline=fgetl(inp);
[a,b]=strtok(tline);
count=str2double(b);

for i=1:4
    tline=fgetl(inp);
end

% read in data
X = fscanf(inp,'%f', [7,count])';

fclose(inp);
rfoot=X(:,3);
lfoot=X(:,4);

% locate frames with print data for left and right
% if the force columns have possitive values for a print
% then the foot was in contact

pl=1;
pr=1;
for i=1:count
    if lfoot(i)>0
        lfeet(pl)=i;
        pl=pl+1;
    end
    if rfoot(i)>0
        rfeet(pr)=i;
        pr=pr+1;
    end
end

[lcount,lext]=count_prints(lfeet,'unused',1);
[rcount,rext]=count_prints(rfeet,'unused',2);

if exist('proc_info.mat','file') == 2
    delete('proc_info.mat');
end
save proc_info infile lcount lext rcount rext count rate
```

```
Lc=lcount;
Rc=rcount;
```

Appendix A1.4: Using the 'noReg' option of the 'Zebris_NoGUI' command in the 'Zebris' in-house toolkit, the pressure records from a trial are extracted from the ASCII file exported from the WIN-FDM treadmill software.

```
% function to build registration groups from proc_info.m and
CutPoints Var

function eyetrackRegSects(bufferWidth)

% load required data

CutPoints=evalin('base','CutPoints');
load('proc_info.mat','rate','lcount','lext','rcount','rext');

% convert CutPoints to frame numbers

numCuts=size(CutPoints);
cutFrames=zeros(numCuts(1),2);

for i=1:numCuts
    cutFrames(i,1)=(CutPoints(i)-bufferWidth)*rate;
    cutFrames(i,2)=(CutPoints(i)+bufferWidth)*rate;
end

% get count of prints in each cut zone

lc=zeros(numCuts(1),2);
rc=zeros(numCuts(1),2);

for i=1:numCuts
    lb=cutFrames(i,1);
    ub=cutFrames(i,2);

    for j=1:lcount
        if lext(j,1)<=lb && lext(j,2)>=lb
            lc(i)=lc(i)+1;
        else
            if lext(j,1)>=lb && lext(j,2)<=ub
                lc(i)=lc(i)+1;
            else
                if lext(j,1)<=ub && lext(j,2)>=ub
                    lc(i)=lc(i)+1;
                end
            end
        end
        if lc(i,1)==1
            lc(i,2)=j;
        end
    end

    for j=1:rcount
        if rext(j,1)<=lb && rext(j,2)>=lb
```

```
            rc(i)=rc(i)+1;
        else
            if rext(j,1)>=lb && rext(j,2)<=ub
                rc(i)=rc(i)+1;
            else
                if rext(j,1)<=ub && rext(j,2)>=ub
                    rc(i)=rc(i)+1;
                end
            end
        end
        if rc(i,1)==1
            rc(i,2)=j;
        end
    end
end

% group prints outside cut zones

lGroups=zeros(numCuts(1)+1,2);
rGroups=zeros(numCuts(1)+1,2);

lGroups(1,1)=1;
rGroups(1,1)=1;
lGroups(1,2)=lc(1,2)-1;
rGroups(1,2)=rc(1,2)-1;

for i=2:numCuts(1)
    lGroups(i,1)=lGroups(i-1,2)+lc(i-1,1)+1;
    lGroups(i,2)=lc(i,2)-1;
    rGroups(i,1)=rGroups(i-1,2)+rc(i-1,1)+1;
    rGroups(i,2)=rc(i,2)-1;

end

lGroups(numCuts(1)+1,1)=lc(numCuts(1),1)+lc(numCuts(1),2);
rGroups(numCuts(1)+1,1)=rc(numCuts(1),1)+rc(numCuts(1),2);
lGroups(numCuts(1)+1,2)=lcount;
rGroups(numCuts(1)+1,2)=rcount;

fprintf('\nCut Zones:\n\n');
fprintf('      Zone    Start Print    Print Count\n')

for i=1:numCuts
    fprintf('Left   %2d         %d
%d\n',i,lc(i,2),lc(i,1));
end
fprintf('\n');
for i=1:numCuts
    fprintf('Right  %2d         %d
%d\n',i,rc(i,2),rc(i,1));
end
fprintf('\n');
fprintf('\nPrint Groups:\n\n');
fprintf('      Group    Start Print    End Print\n')
for i=1:numCuts+1
    fprintf('Left    %2d         %3d
%d\n',i,lGroups(i,1),lGroups(i,2));
end
fprintf('\n');
for i=1:numCuts+1
```

```
    fprintf('Right   %2d          %3d
%d\n',i,rGroups(i,1),rGroups(i,2));
end

save groups lGroups rGroups

%disp(lc)
%disp(rc)
%disp(lGroups)
%disp(rGroups)
```

Appendix A1.5: MATLAB script that uses the CutPoints variable defined from the previous step alongside the treadmill pressure record output (Proc Info) to group the prints into those made during different types of visual tracking. The output is a list of start and end pressure records in each group for left and right feet are saved.

```
% function to load the appropriate prints based on the contents of
lGroups
% & rGroups

function eyetrackLoadPrints()

% creat lists of print numbers

load groups

a=size(lGroups);
numGroups=a(1);

%left prints
lpc=zeros(numGroups,1);
for i=1:numGroups
    k=0;
    for j=lGroups(i,1):lGroups(i,2)
        lp(i,k+1)=lGroups(i,1)+k;
        %fprintf('%d ',lGroups(i,1)+k);
        k=k+1;
    end
    lpc(i)=k;
    %fprintf('\n');
end

%right prints
rpc=zeros(numGroups,1);
for i=1:numGroups
    k=0;
    for j=rGroups(i,1):rGroups(i,2)
        rp(i,k+1)=rGroups(i,1)+k;
        %fprintf('%d ',rGroups(i,1)+k);
        k=k+1;
    end
    rpc(i)=k;
    %fprintf('\n');
end

% load prints
```

```
% left
for i=1:numGroups
    evalstr='LeftGrp';
    if i<10
        evalstr=strcat(evalstr,'0');
    end
    pstart=lp(i,1);
    for j=1:lpc(i)
        evalstr2=evalstr;

evalstr2=strcat(evalstr2,num2str(i),'(',num2str(j),').P=load(''','LP
_P_');
        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end


evalstr2=strcat(evalstr2,num2str(pstart),'.mat''',',',''''LP_P_');

        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end

        evalstr2=strcat(evalstr2,num2str(pstart),''');');

        eval(evalstr2);
        %fprintf('%s\n',evalstr2);
        pstart=pstart+1;
    end
end

% right
for i=1:numGroups
    evalstr='RightGrp';
    if i<10
        evalstr=strcat(evalstr,'0');
    end
    pstart=rp(i,1);
    for j=1:rpc(i)
        evalstr2=evalstr;

evalstr2=strcat(evalstr2,num2str(i),'(',num2str(j),').P=load(''','RP
_P_');
        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end
```

```
evalstr2=strcat(evalstr2,num2str(pstart),'.mat''',',',''''RP_P_');

        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end

        evalstr2=strcat(evalstr2,num2str(pstart),''');');

        eval(evalstr2);
        %fprintf('%s\n',evalstr2);
        pstart=pstart+1;
    end
end

% find largest array
gs=[0,0];

% left
for i=1:numGroups
    evalstr='psize=size(LeftGrp';
    if i<10
        evalstr=strcat(evalstr,'0');
    end
    evalstr=strcat(evalstr,num2str(i));
    pstart=lp(i,1);
    for j=1:lpc(i)
        evalstr2=evalstr;
        evalstr2=strcat(evalstr2,'(',num2str(j),')','.P.LP_P_');
        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end
        evalstr2=strcat(evalstr2,num2str(pstart),');');
        eval(evalstr2);
        pstart=pstart+1;
        if psize(1)>gs(1)
            gs(1)=psize(1);
        end
        if psize(2)>gs(2)
            gs(2)=psize(2);
        end
    end
end

% right
for i=1:numGroups
    evalstr='psize=size(RightGrp';
    if i<10
        evalstr=strcat(evalstr,'0');
    end
    evalstr=strcat(evalstr,num2str(i));
    pstart=rp(i,1);
```

```
    for j=1:rpc(i)
        evalstr2=evalstr;
        evalstr2=strcat(evalstr2,'(',num2str(j),')','.P.RP_P_');
        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end
        evalstr2=strcat(evalstr2,num2str(pstart),');');
        eval(evalstr2);
        pstart=pstart+1;
        if psize(1)>gs(1)
            gs(1)=psize(1);
        end
        if psize(2)>gs(2)
            gs(2)=psize(2);
        end
    end
end

% convert to pImage stacks

for i=1:numGroups
    % process right first
    l=1;
    evalstr='P=RightGrp';
    if i<10
        evalstr=strcat(evalstr,'0');
    end
    evalstr=strcat(evalstr,num2str(i));
    pstart=rp(i,1);
    grpName='Group';
    grpName=strcat(grpName,num2str(i));
    for j=1:rpc(i)
        evalstr2=evalstr;
        evalstr2=strcat(evalstr2,'(',num2str(j),')','.P.RP_P_');
        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end
        evalstr2=strcat(evalstr2,num2str(pstart),';');
        eval(evalstr2);
        PP=pImage2D(P);
        PP=resize(PP,gs);

        pstart=pstart+1;
        storeName=grpName;
        storeName=strcat(storeName,'(',num2str(l),')=PP;');
        l=l+1;
        eval(storeName);
        %fprintf('%s\n',storeName);

    end

    evalstr='P=LeftGrp';
```

```
    if i<10
        evalstr=strcat(evalstr,'0');
    end
    evalstr=strcat(evalstr,num2str(i));
    pstart=lp(i,1);
    grpName='Group';
    grpName=strcat(grpName,num2str(i));
    for j=1:lpc(i)
        evalstr2=evalstr;
        evalstr2=strcat(evalstr2,'(',num2str(j),')','.P.LP_P_');
        if pstart<10
            evalstr2=strcat(evalstr2,'00');
        else
            if pstart<100
                evalstr2=strcat(evalstr2,'0');
            end
        end
        evalstr2=strcat(evalstr2,num2str(pstart),';');
        eval(evalstr2);
        P=flipud(P);
        PP=pImage2D(P);
        PP=resize(PP,gs);

        pstart=pstart+1;
        storeName=grpName;
        storeName=strcat(storeName,'(',num2str(l),')=PP;');
        l=l+1;
        eval(storeName);
        %fprintf('%s\n',grpName);
    end

    astring='assignin(';

astring=strcat(astring,char(39),'base',char(39),',',char(39),grpName
,char(39),',',grpName,');');
    eval(astring);
end
```

Appendix A1.6: Based on the groups of pressure records defined in the previous step, the arrays of prints are then built and stored in pImage2D format. These groups can then be combined to form overall arrays of pressure records made during different conditions and are now ready for analysis using pSPM.

```
Pr1=registerWS(P(1),P);

M=mean(Pr1);'

Pr2=registerWS(M,P);
```

Appendix A1.7: MATLAB script to conduct a within subject registration within in-house pSPM toolkit where 'P' is the array of records. Returns prints registered to the first record in the array (Pr1), and then re-registers to the mean pressure profile from this registration to avoid bias (Pr2).

```
Pr2Thresholded=threshold(Pr2,1);

MeanPrint=mean(Pr2Thresholded);
```

```
MeanPrintThresholded=threshold(MeanPrint,1);

PThresholded_Reg=registerWS(MeanPrintThresholded,Pr2Thresholded);
```

Appendix A1.8: MATLAB script to complete a thresholded registration on a pre-registered sample of pressure records where 'P' is the array of records.

```
% QtrackTools - Get data from TSV file
%
% [names,nodes]=qtReadTSV(tsvInputFile);
% Input = string label for disk file
%
% Outputs: names=struct containing Marker Names
%          data=MxN matrix of marker positions M=Number of Frames
%                                              N=Number of Markers *
3

function[markerList,markerData]=qtReadTSV(tsvInput)

% open input file
% No error checking will fail if file name invalid
inp=fopen(tsvInput,'r');

% get number of frames
tline=fgets(inp);
l=size(tline);
f=substr(tline,13,l(2)-13);
frames=str2double(f);

fprintf('Frame Count = %d\n',frames)

% get number of cameras
tline=fgets(inp);
l=size(tline);
f=substr(tline,14,l(2)-14);
cameras=str2double(f);

fprintf('Camera Count = %d\n',cameras)

% get number of markers
tline=fgets(inp);
l=size(tline);
f=substr(tline,14,l(2)-14);
markers=str2double(f);

fprintf('Marker Count = %d\n',markers)

% get sample frequency
tline=fgets(inp);
l=size(tline);
f=substr(tline,10,l(2)-10);
frequency=str2double(f);
```

```
fprintf('Samples per Second = %d\n',frequency)

% currently ignore Analog info as not used

for i=1:6
    tline=fgets(inp);
end

% check that line is correct and extract names
str=substr(tline,1,12);
if strcmp(str,'MARKER_NAMES')

    % get Number of Markers
    l=size(tline);
    numMarkers=1;
    for i=14:l(2)
        if tline(i)==9
            numMarkers=numMarkers+1;
        end
    end

    % get marker divisions
    p=zeros(numMarkers+1,1);
    k=1;
    for i=1:l(2)
        if tline(i)==9
            p(k)=i;
            k=k+1;
        end
    end
    p(k)=l(2);

    % put marker names into cell
    c=cell(1,numMarkers);
    for i=1:numMarkers
        if i<numMarkers
            str=substr(tline,p(i)+1,p(i+1)-p(i)-1);
        else
            str=substr(tline,p(i)+1,p(i+1)-p(i));
        end
        c{i}=str;
    end

    markerList=c;
else
    markerList=-1;
    return
end

% put data into array

markerData=zeros(frames,numMarkers*3);

% fill array
for k=1:frames
    markerData(k,:)=fscanf(inp,'%f',numMarkers*3);
end
```

```
% close input file
fclose(inp);
```

Appendix A1.9: MATLAB script to read in data from the TSV file. Firstly information regarding camera number, marker number, marker names and capture frequency is identified. Marker names are then stored in a list and the global coordinate data for each stored in a matrix.

```
% qtDisplayNames - Display the maker names and numbers read from tsv
file

function qtDisplayNames(names)

numMarkers=size(names);

fprintf('\n');
for i=1:numMarkers(2)
    fprintf('Marker Number: %d %s %s\n',i,9,names{i});
end
```

Appendix 1.10: MATLAB script to display marker names and numbers in a variable.

```
% function to calculate 2 Point angles with a major axis

function[angle]=qtCalc2PointAngle(pointA,pointB,data,AXIS)

pAx=data(:,((pointA-1)*3)+1);
pAy=data(:,((pointA-1)*3)+2);
pAz=data(:,((pointA-1)*3)+3);

pBx=data(:,((pointB-1)*3)+1);
pBy=data(:,((pointB-1)*3)+2);
pBz=data(:,((pointB-1)*3)+3);

a=size(pAx);

angle=zeros(a(1),1);

for i=1:a(1)
    switch AXIS
        case 'XaY'
            pa=[pAx(i),pAy(i),0];
            pb=[pBx(i),pBy(i),0];
            pc=[pBx(i),pAy(i),0];
        case 'XaZ'
            pa=[pAx(i),0,pAz(i)];
            pb=[pBx(i),0,pBz(i)];
            pc=[pBx(i),0,pAz(i)];
        case 'YaZ'
            pa=[0,pAy(i),pAz(i)];
```

```
            pb=[0,pBy(i),pBz(i)];
            pc=[0,pBy(i),pAz(i)];
        case 'XYaZ'
            pa=[pAx(i),pAy(i),pAz(i)];
            pb=[pBx(i),pBy(i),pBz(i)];
            pc=[pBx(i),pBy(i),pAz(i)];
        case 'XZaY'
            pa=[pAx(i),pAy(i),pAz(i)];
            pb=[pBx(i),pBy(i),pBz(i)];
            pc=[pBx(i),pBy(i),pBz(i)];
        case 'YZaX'
            pa=[pAx(i),pAy(i),pAz(i)];
            pb=[pBx(i),pBy(i),pBz(i)];
            pc=[pAx(i),pBy(i),pAz(i)];
        otherwise
            return
    end

    v21=[pa(1)-pb(1),pa(2)-pb(2),pa(3)-pb(3)];
    v23=[pc(1)-pb(1),pc(2)-pb(2),pc(3)-pb(3)];
    angle(i) = 180/pi*(atan2(norm(cross(v21,v23)),dot(v21,v23)));
end
```

Appendix A1.11: MATLAB script to calculate an angle between two markers (point A, point B) for a given trial (data) and relative to an axis (XY, XZ,YZ).

UNIVERSITY OF LIVERPOOL

Department of Musculoskeletal Biology II, Institute of Aging and Chronic Disease

PREMOG

PRIMATE EVOLUTION AND MORPHOLOGY RESEARCH GROUP

Energy costs, External Forces, Limb Motion and Gaze Control in Human Bipedal Gaits

Participant Information Sheet Version 4, 4 March 2011

You are being invited to participate in a research study. Before you decide whether to participate, it is important for you to understand why the research is being done and what it will involve. Please take time to read the following information carefully and feel free to ask us if you would like more information or if there is anything that you do not understand. Please also feel free to discuss this with your friends, relatives and GP if you wish. We would like to stress that you do not have to accept this invitation and should only agree to take part if you want to.

Human walking depends entirely on the ability of the foot, our most unique anatomical feature, to exert the appropriate pressures and point forces against the ground, at the appropriate phase of gait, to decelerate, balance and accelerate the body. We therefore need to understand how the forces and pressures which develop under the foot are related to motion of the upper body, and what energetic costs are imposed on the body by different gaits and substrates, at different speeds, on different slopes, and different surfaces, and sometimes carrying different loads.

We are asking subjects to participate who have no recent injuries to their legs or feet, are free from diabetes, and who are of normal or better fitness. Please ask your GP if you have any doubts about your ability to participate. Some 30 people will be taking part in this study. In some cases you may be asked to participate by a fellow student who is doing an Honours project in our lab. You should feel under no pressure to participate and are free to withdraw at any time and do not need to give an explanation for withdrawing. Results up to the period of withdrawal may be used, if you are happy for this to be done. Otherwise you may request that they are destroyed and no further use is made of them. You may agree to all or only some of the procedures you may be asked to participate in, indicated by different numbers and capital letters below (A-H).In this study we are using pressure and force-sensitive plates and treadmills to measure point forces and pressures exerted by our volunteers in a variety of different gaits, at a variety of speeds and slopes, while tracking the motion of the segments of the upper body using 12 cameras capable of tracking 3D motion of reflective markers. Subjects are usually asked to walk barefoot, as wearing shoes changes the forces applied to the ground in a different way according to the stiffness and shape of individual shoes, and there is risk from slipping if you wear socks or stockings. But in condition D below, we may ask you to wear light footwear containing a pressure sensitive insole. We will ask you to agree to attachment of several reflective markers using sticky tape over important surface markings on the skin, representing bony landmarks, by a same-sex researcher. If you prefer, you can attach them yourself under our supervision. We ask you to wear a t-shirt and sports shorts or similar clothes which do no obstruct the cameras from tracking the surface markers. You will then be able to practice walking over the plates or on the treadmill until you feel comfortable with the experimental setup, before we start recording. We will need about 10 trials in each type of gait, which should take about 2 hours per person on the static plates: much less on the treadmills.

1.When walking on either the pressure or point-force treadmill you should wear the emergency waist cord which will stop the treadmill immediately should you stumble or fall. A large red stop button is easily accessible to you should you wish to stop the treadmill at any time. But when walking on either treadmill at near running speed, or running, you should also wear the safety harness which will be

provided. This is attached by an arrest mechanism like a car seatbelt to an overhead gantry which can support you fully, should you slip, fall or stumble.

2. In this *alternative* study we are looking at the formation of footprints in sands or muds under the pressure formed under the feet. These may be carried out: a) in the laboratory, using an instrumented walkway covered with sand or mud; b) under carefully monitored field conditions, on a beach or mudflat. In this case, strict limitations are placed on recording conditions to ensure safety, and work will only take place during the ebbing of tides and in dry, warm weather.

Additional conditions for the above

A) While walking or running you may be asked to wear a wireless heartrate sensor over your chest. We may record from this as well if you consent.

B) While walking or running, you may be asked to wear a facemask and light, self-contained recording equipment to record your breathing, oxygen use and carbon dioxide production and hence metabolic rate/energy consumption. This procedure will be demonstrated to you in advance of consent and should cause you no discomfort. If it does, you should inform the researchers, and you may withdraw at any time.

C) While walking or running, you may be asked to carry loads of up to 10 kg asymmetrically, that is on one side of your body, in which case they will take the form of light loads such as sticks in the hand; dumb-bells, or fire-service training human dummies; or symmetrically, in which case they will consist of weighted waistcoats, securable by straps

D) While walking or running, we may ask you to wear light footwear containing instrumented pressure-sensitive insoles

E) While walking or running, you may be asked to allow surface electromyography sensors, positive and negative, to be attached to the skin over important muscles, so we can record muscle activity

F) While walking or running, you may be asked to wear either or both: a helmet or headset carrying miniature video cameras to record your eye movements, while we ask you to look at distant or close-up markers or objects in front of you.

G) While walking or running, you may be asked to allow very small, light force sensors called accelerometers to be attached to your head, limbs or body using lightweight Velcro straps Additionally, and separately you may be asked to permit recording of deep structures in the sole of your feet, such as the plantar aponeurosis, using ultrasound. This involves applying a harmless, stain-free hair-gel like substance to your foot, and passing an ultrasound probe over the foot or resting your foot against a plate in which the probe is mounted. You may also be asked to permit recording of the shape of your feet, using a low power and harmless laser scanner, but you should take care not to stare into the beam

The recording equipment will be controlled by the researchers: these may include senior lecturer Dr. Nathan Jeffery, Mr. Russell Savage (PREMOG's Research Officer), postdoctoral research fellow Dr. Karl Bates, postgraduate students including Katy Wareing, Emma Webster and Sarita Morse, and Honours Students who are participating in the project as part of their Honours dissertation. They will tell you what gaits they would like you to use, and what speeds, and will help you practice them until you are comfortable with the exercise.

If you are happier with having only same-sex researchers in the lab while you are doing the exercises, by all means let us know.

We cannot usually offer any payments, but in some circumstances may be able to help with reasonable travel expenses if incurred by your participation. Please let us know in advance if you will need such assistance. There are no benefits to you from taking part other than participation in an exercise which may inform you about how you yourself walk, stand or run. All participants taking part in this and other University of Liverpool studies are covered for negligent and non-negligent harm by the University's Clinical Trials Insurance policy.Foot pressure and force records, and motion-tracking

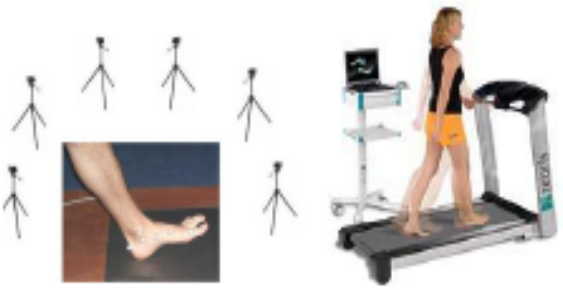
data will be held anonymously. However, please ask if you would like to be given a copy of any publication or a copy or movies of your recordings if you wish: but in this case we will need to keep your name and email in a coded form (the name and code being accessible only to the senior Principal Investigator) so that your name and email address can be associated with your data for this purpose only, after which time the name and address will be erased. We do ask you to tell us your age, height and weight – or we can measure your height and weight for you. The data will be held on computers in this laboratory for this and future, related PREMOG projects. If you want your data securely erased after analysis, please let us know in advance.

The data will be analyzed and written up anonymously by researchers, and may then be published.

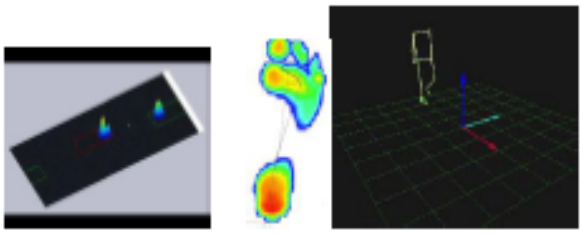
If you are unhappy, or if there is a problem, please feel free to let us know by contacting [Robin Huw Crompton 07970 570433] and we will try to help. If you remain unhappy or have a complaint which you feel you cannot come to us with then you should contact the Research Governance Officer on 0151 794 8290 (ethics@liv.ac.uk). When contacting the Research Governance Officer, please provide details of the name or description of the study (so that it can be identified), the researcher(s) involved, and the details of the complaint you wish to make.

If you have any queries concerning this study, please contact the Senior Principal Investigator, Professor Robin Crompton on 051 794 5500, rhcromp@liv.ac.uk We would be happy to show you round the lab if it would help you make up your mind whether to participate. Many thanks in advance for your participation in our research, which will be invaluable.

Experimental equipment for basic protocol



6-12 motion-capture cameras markers track the motion of reflective markers placed over bony landmarks on the foot and upper body, while the subject walks along a walkway and across a pressure and/or force sensitive plate like this one, or on a treadmill such as that above left



The resulting data: left: foot-pressure records show high pressure areas as 'peaks' and/or as 'hot' colours.
Right: a computer reconstructs body motion during walking as a stick-figure. Data from other, less often used techniques such as EMG or ultrasound can be shown to you on request before consent or participation.

Experimental equipment for further conditions

Above, left: gaze tracking goggles; middle: gaze tracking helmet. Note that the equipment is designed not to block your vision! Above, right, an accelerometer similar to that you may be asked to wear

One of our subjects walking on our point-force measuring treadmill, wearing the oxygen-consumption measuring equipment we may ask you to wear

Appendix A1.12: Participant Information Form

UNIVERSITY OF LIVERPOOL

Committee on Research Ethics

CONSENT FORM

Title of Research Project:

Energy Costs, External Forces, Limb Motion and Gait Control in Human Bipedal Gaits

Please circle as appropriate Protocols/Conditions requested and agreed to:

1 2 A B C D E F G

Please initial box

Researcher(s): **Prof. R.H. Crompton** (Lead Researcher/PI) Dr. Nathan Jeffery, Mr. Russell Savage, Dr. Karl Bates, Ms. Emma Webster, Ms. Sarita Morse and others

1. I confirm that I have read and have understood the information sheet dated 4 March 2011 for the above circled studies/conditions/protocols. I have had the opportunity to consider the information, ask questions and have had these answered satisfactorily. ☐

2. I understand that my participation is voluntary and that I am free to withdraw at any time without giving any reason, without my rights being affected. ☐

3. I understand that, under the Data Protection Act, I can at any time ask for access to the information I provide and I can also request the destruction of that information if I wish. ☐

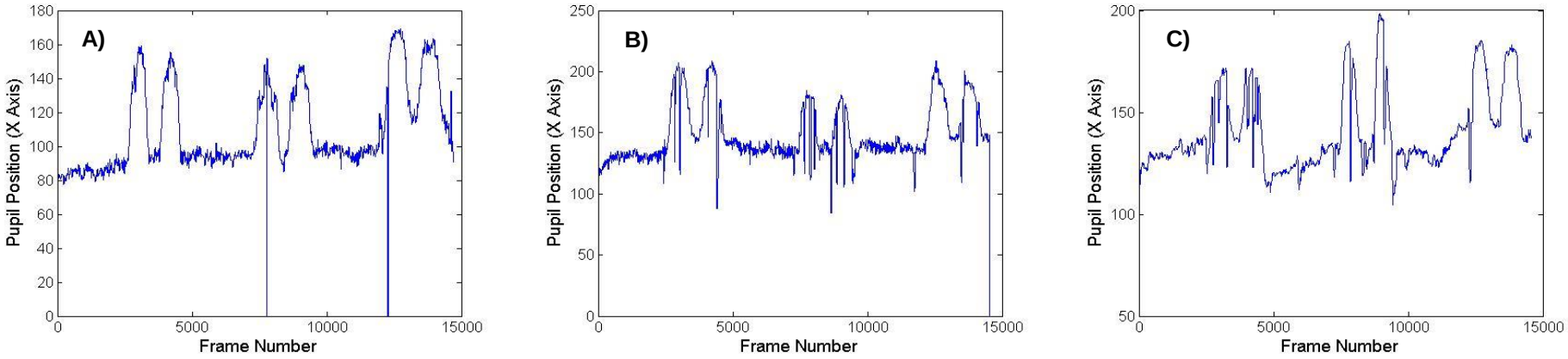
4. I agree that, if required, a third party (for example, my General Practitioner) may be contacted about my participation in this research. ☐

Participant Name	Date	Signature
Name of Person taking consent	Date	Signature
Lead Researcher	Date	Signature

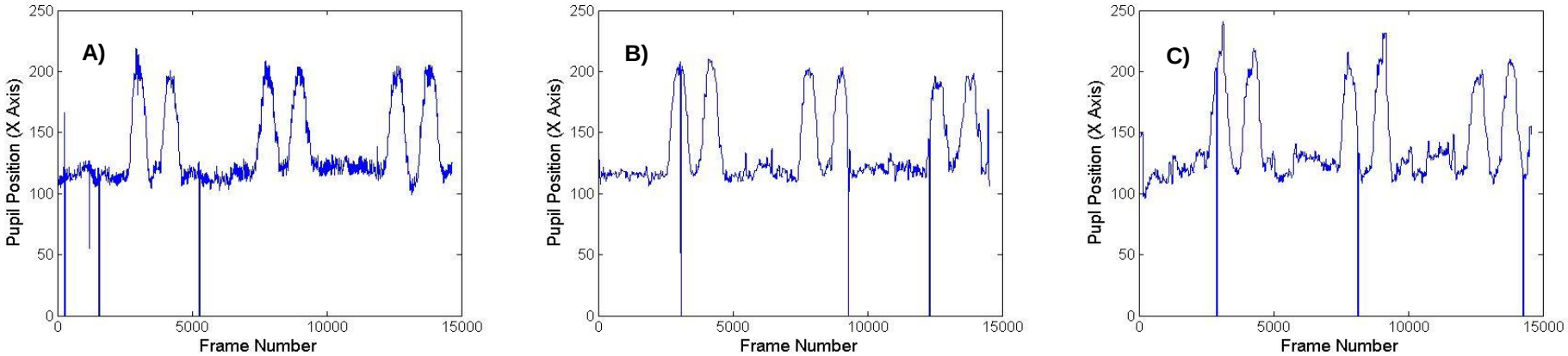
The contact details of lead Researcher (Principal Investigator) are:
Professor Robin Huw Crompton, Institute of Aging and Chronic Disease,The University of Liverpool, Ashton Street, Liverpool L69 3GE email: rhcromp @liv.ac.uk; work phone 0151794 5500; website www.liv.ac.uk/premog
Version 4 March 2011 RHC

Appendix 2: Supplementary Information for Chapter 3

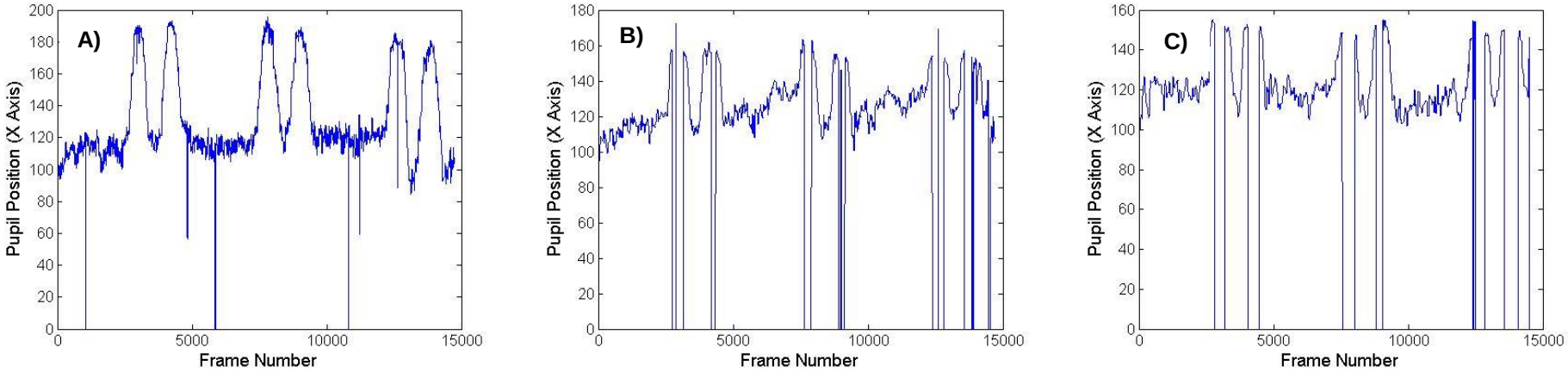
This Appendix contains Eye Tracking and Foot Pressure mean square error profiles associated with Chapter 3.



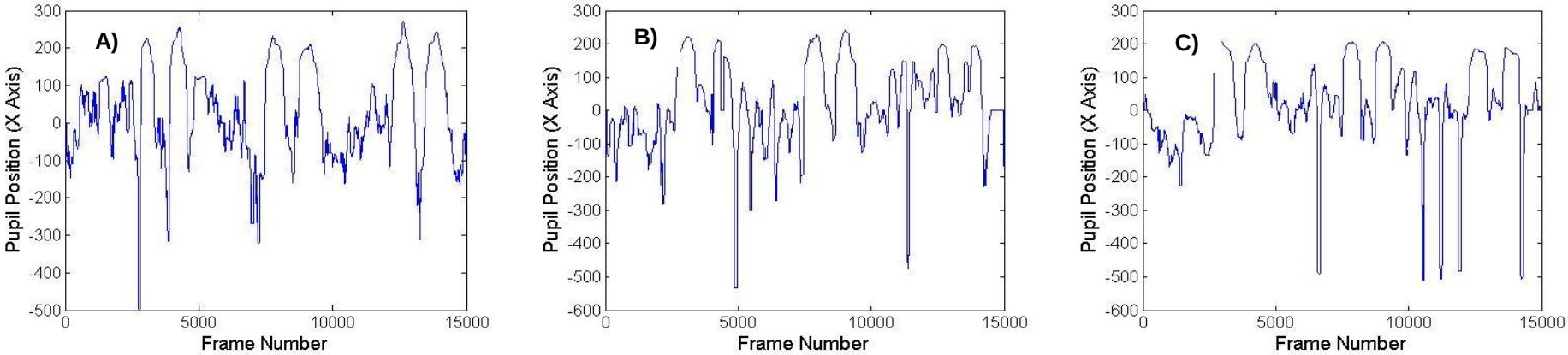
Appendix A2.1: Subject 1 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



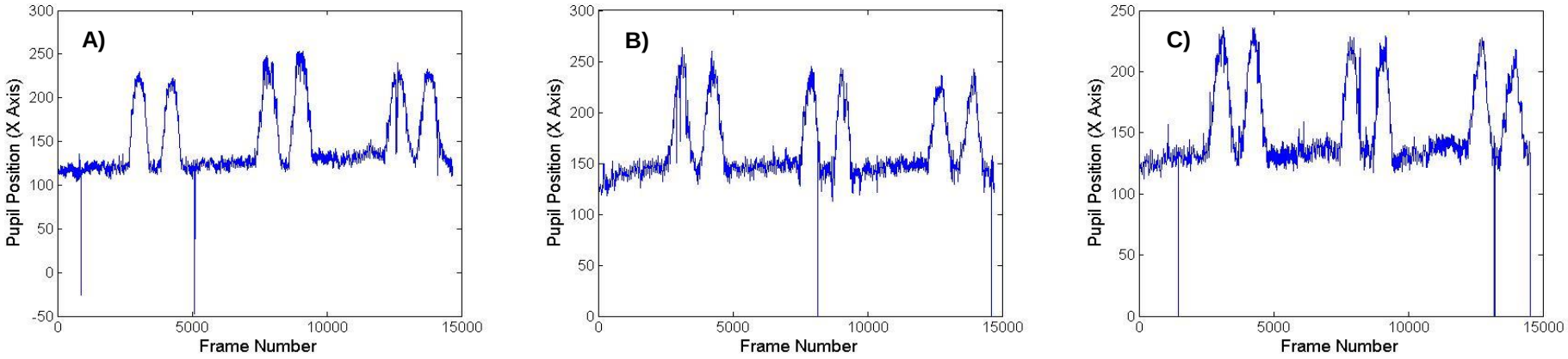
Appendix A2.2: Subject 2 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



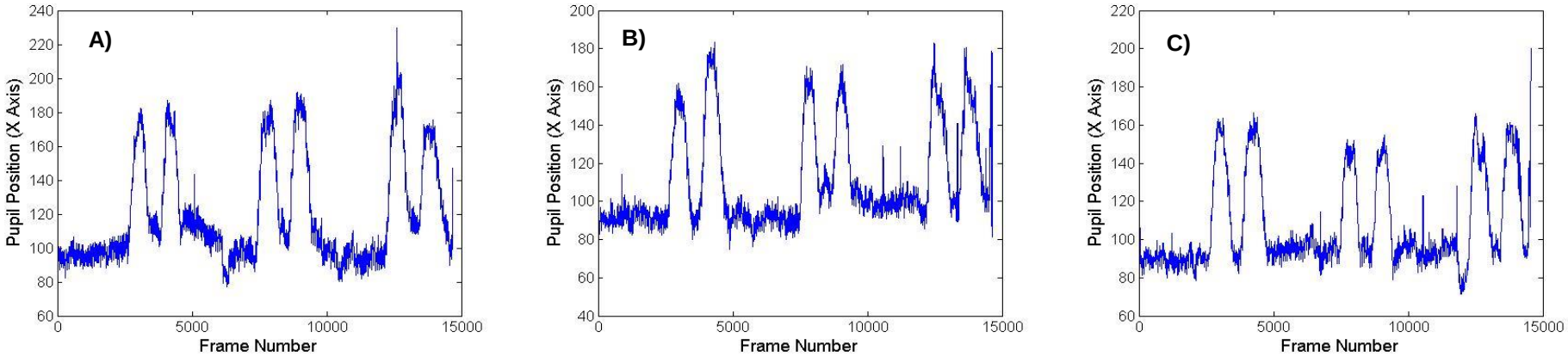
Appendix A2.3: Subject 3 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



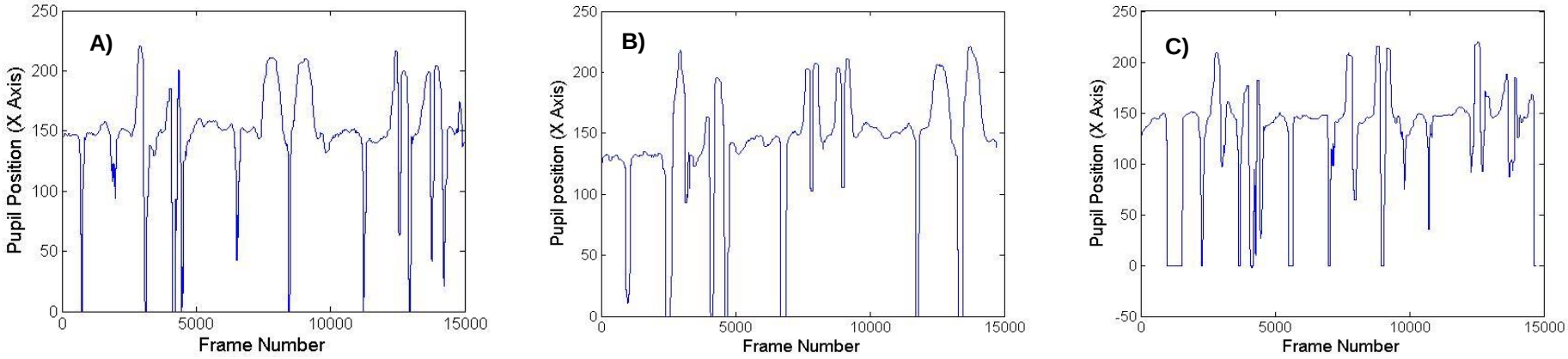
Appendix A2.4: Subject 4 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



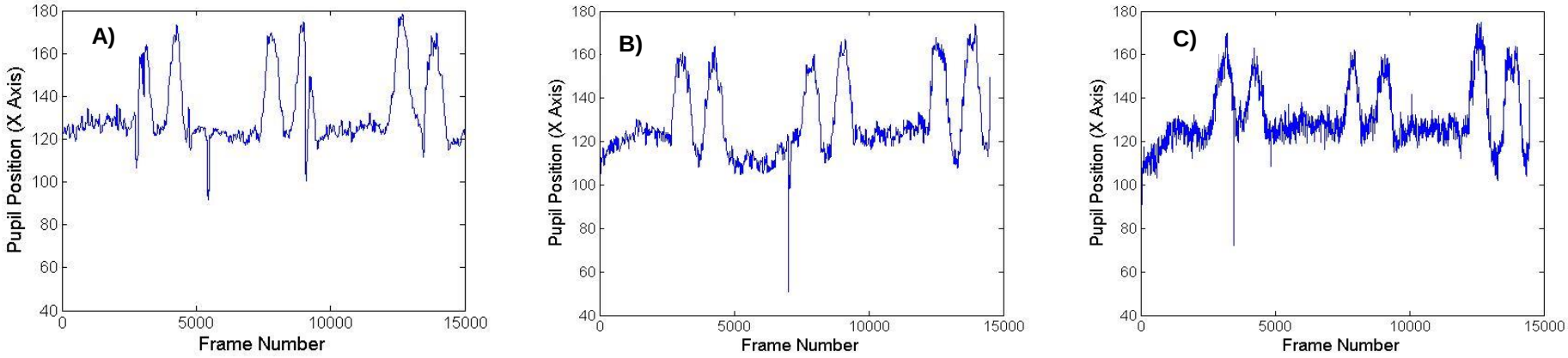
Appendix A2.5: Subject 5 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



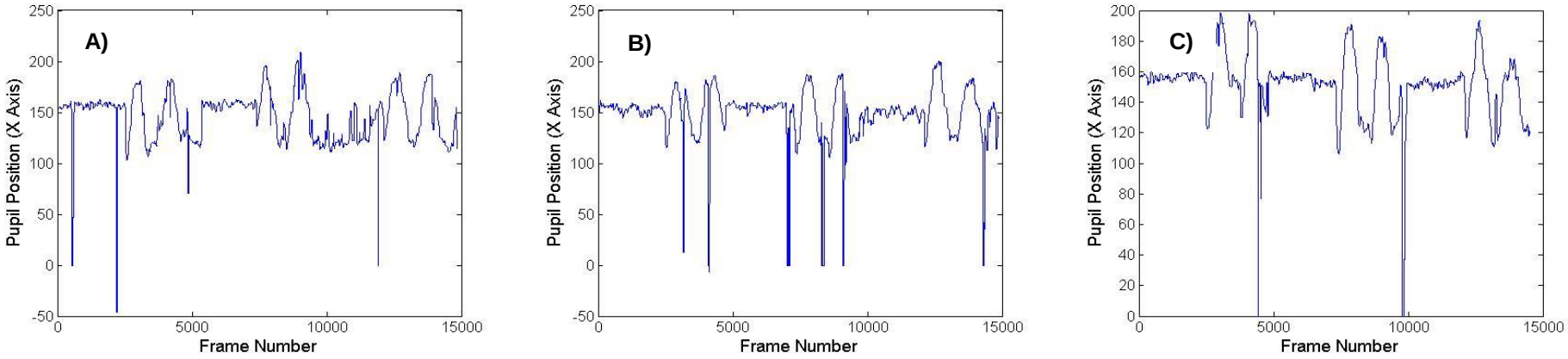
Appendix A2.6: Subject 6 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



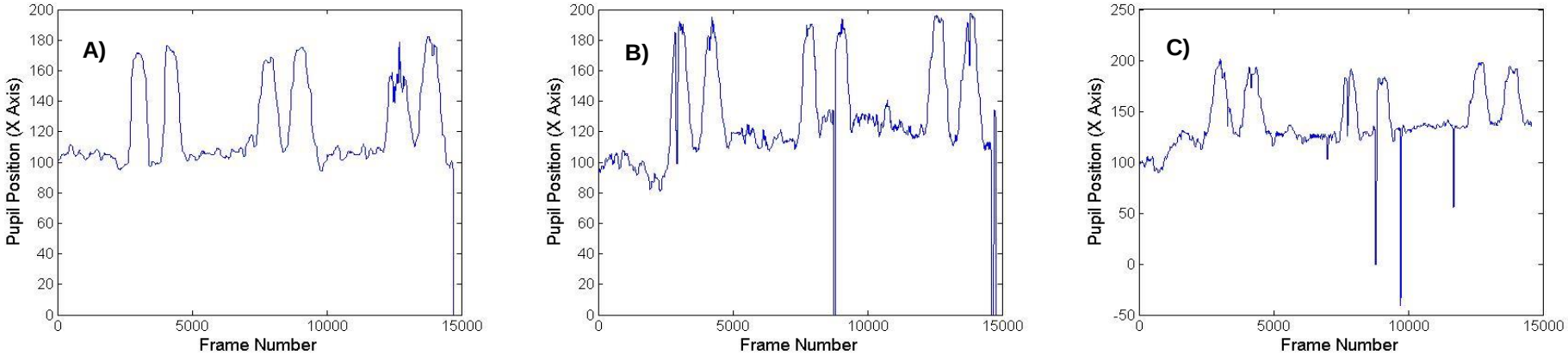
Appendix A2.7: Subject 7 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



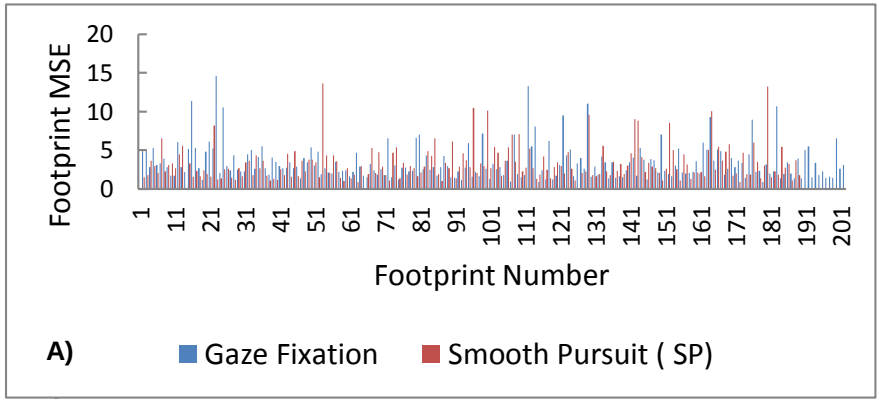
Appendix A2.8: Subject 8 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.

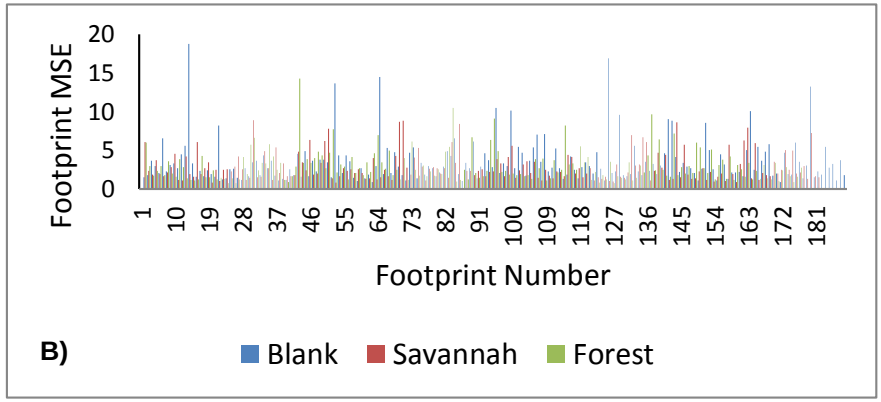


Appendix A2.9: Subject 9 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.

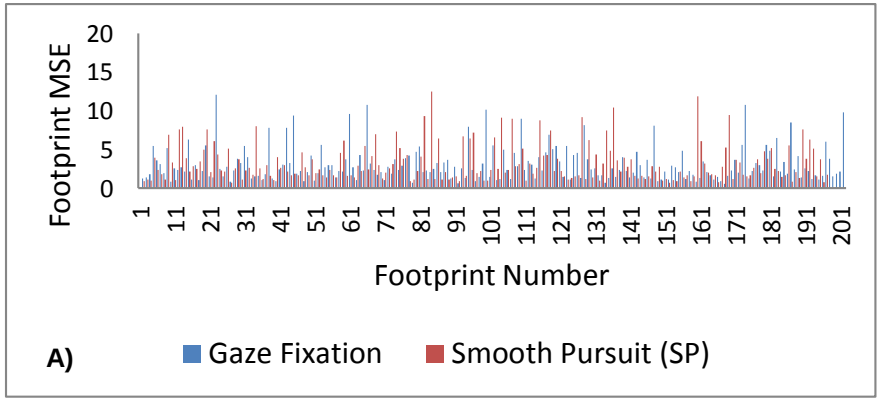


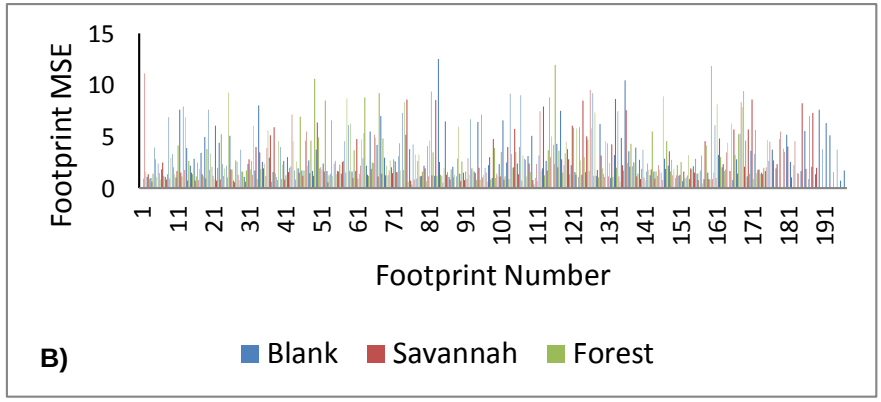
Appendix A2.10: Subject 10 Eye Tracker Profiles when tracking on the blank (A), savannah (B), and forest scene (C). Pupil position was measured in the X (horizontal) plane.



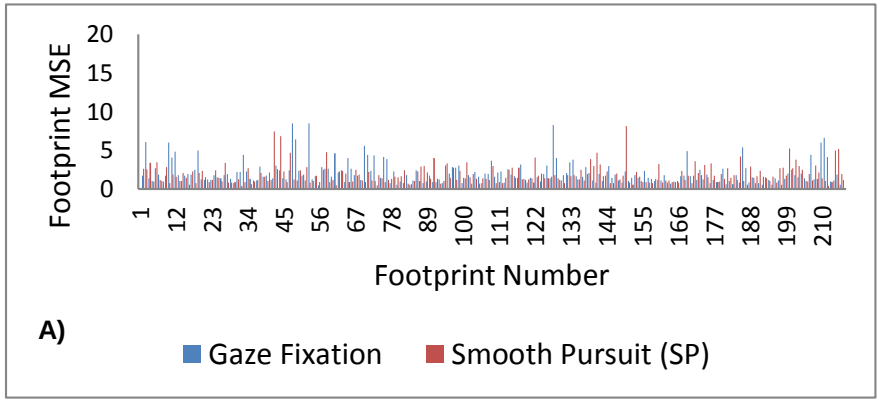


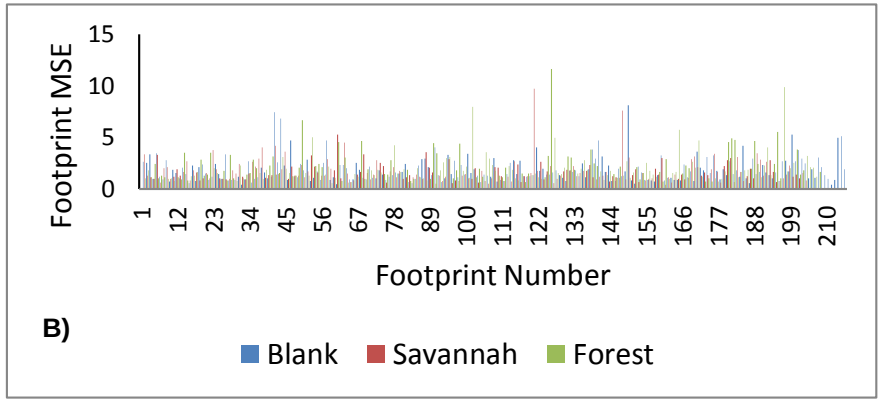
Appendix A2.11: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 1.



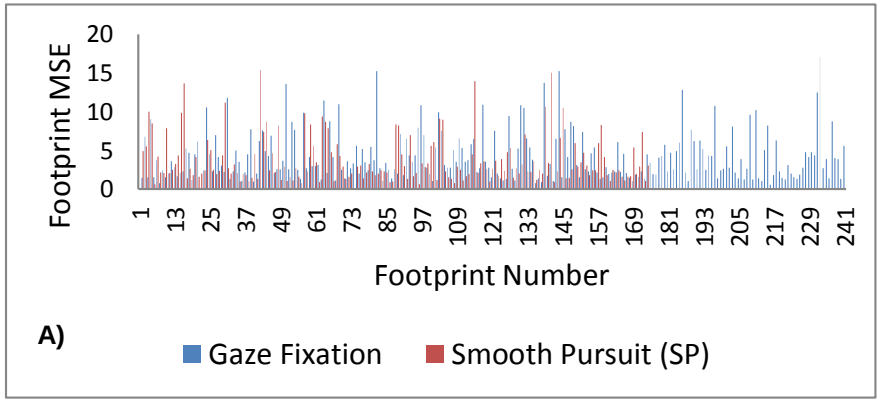


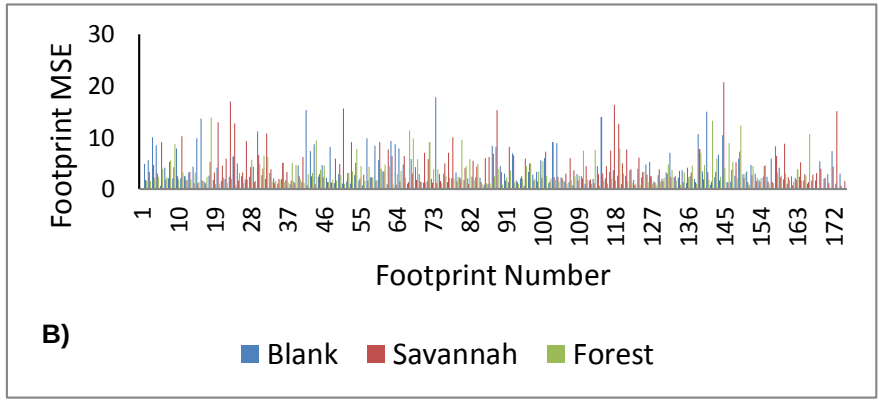
Appendix A2.12: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 2.



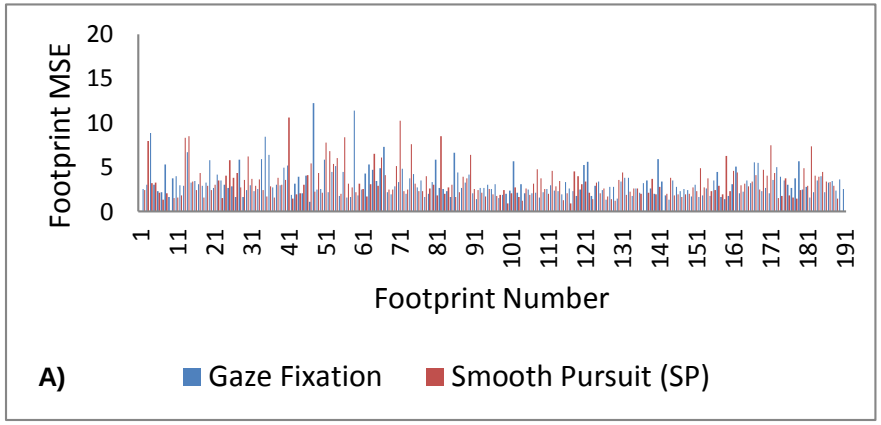


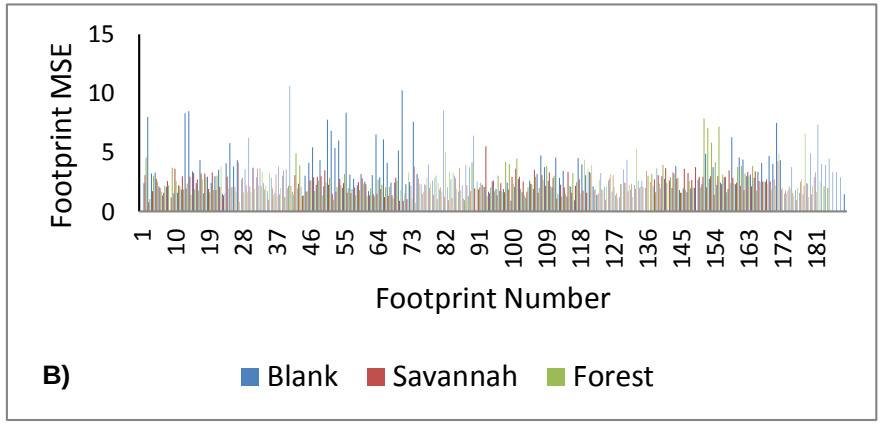
Appendix A2.13: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 3.



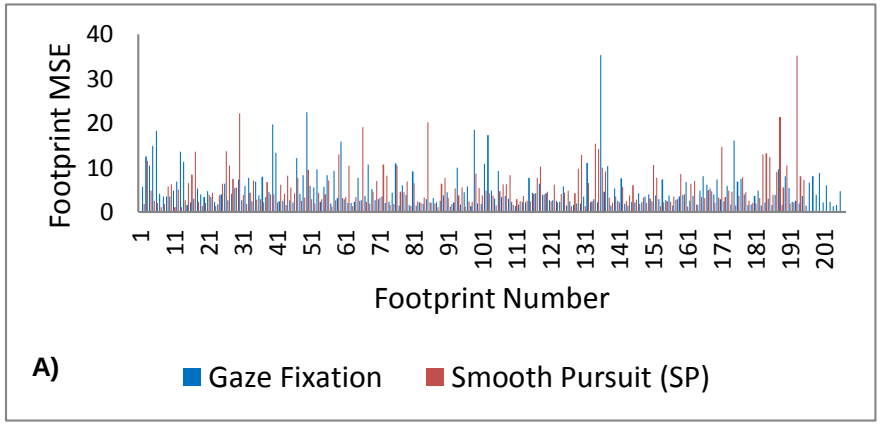


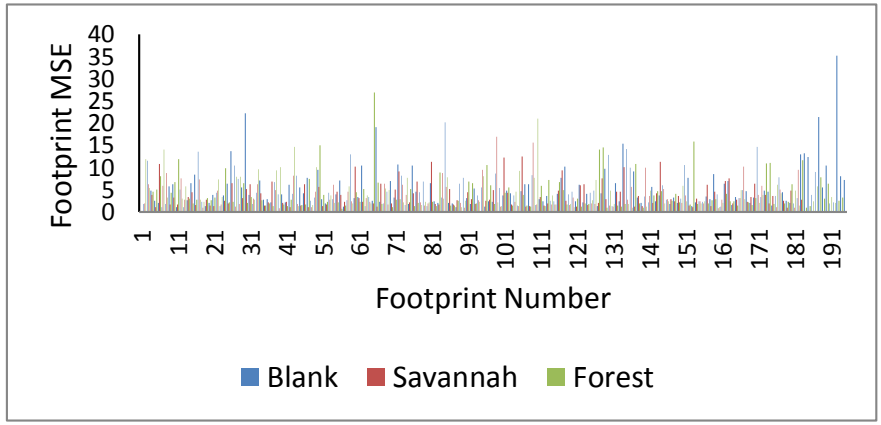
Appendix A2.14: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 4.



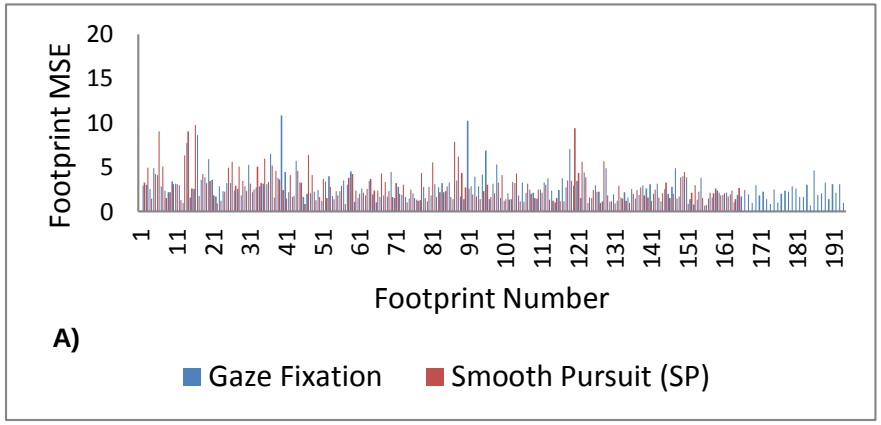


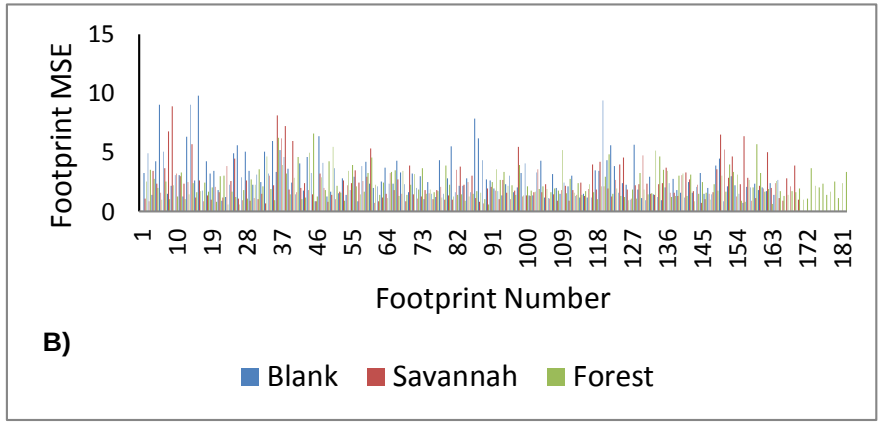
Appendix A2.15: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 5.



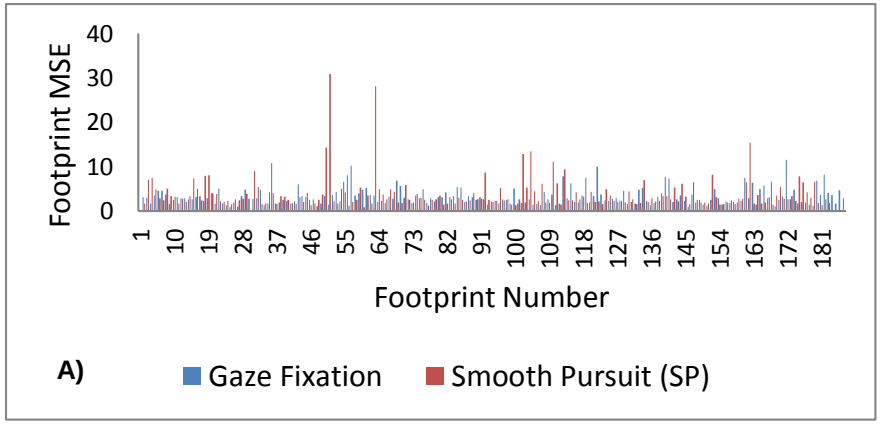


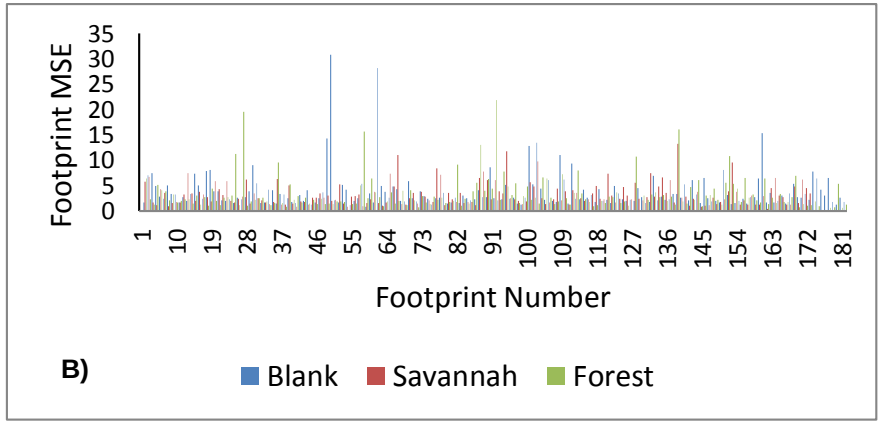
Appendix A2.16: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 6.



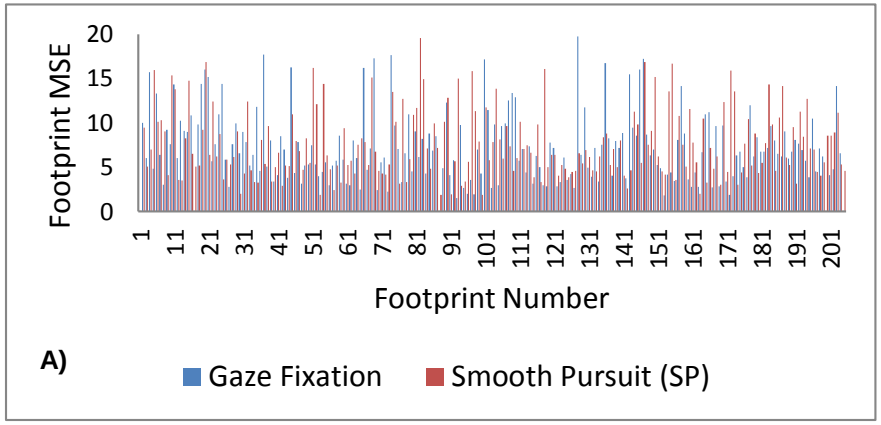


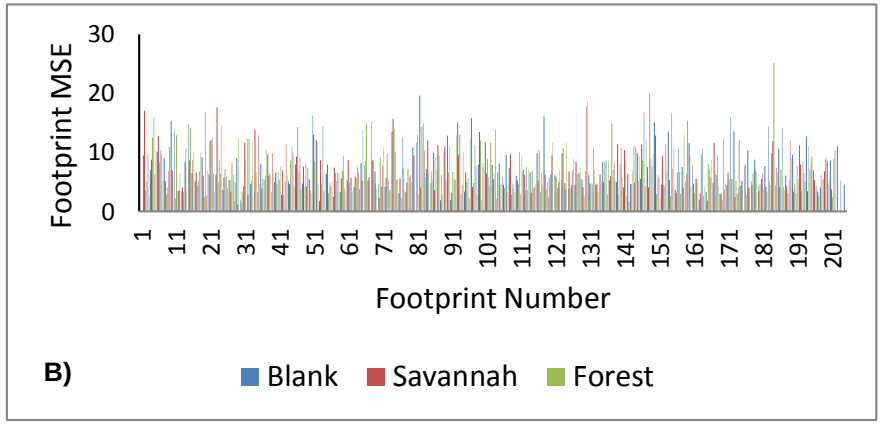
Appendix A2.17: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 7.



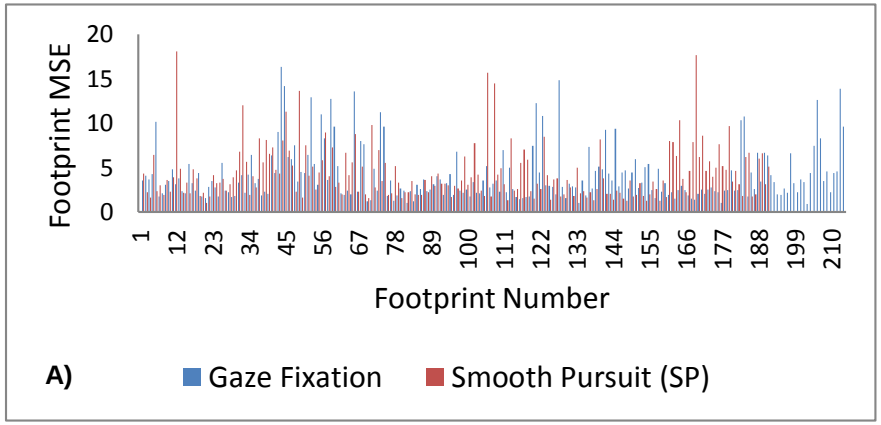


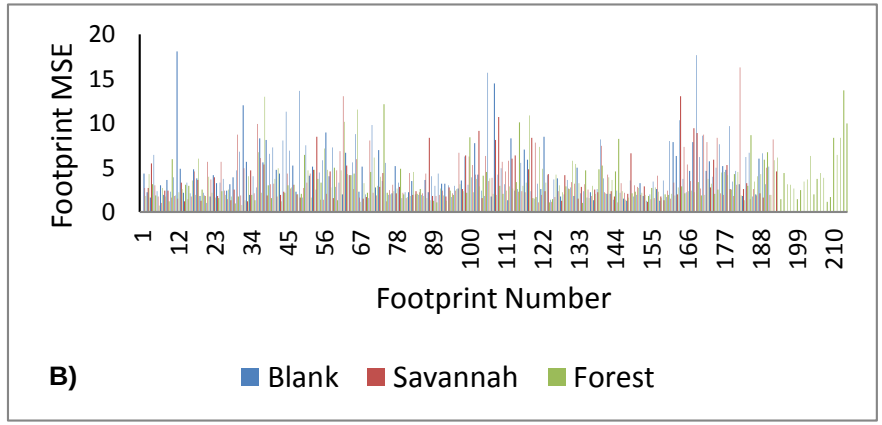
Appendix A2.18: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 8.





Appendix A2.19: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 9.

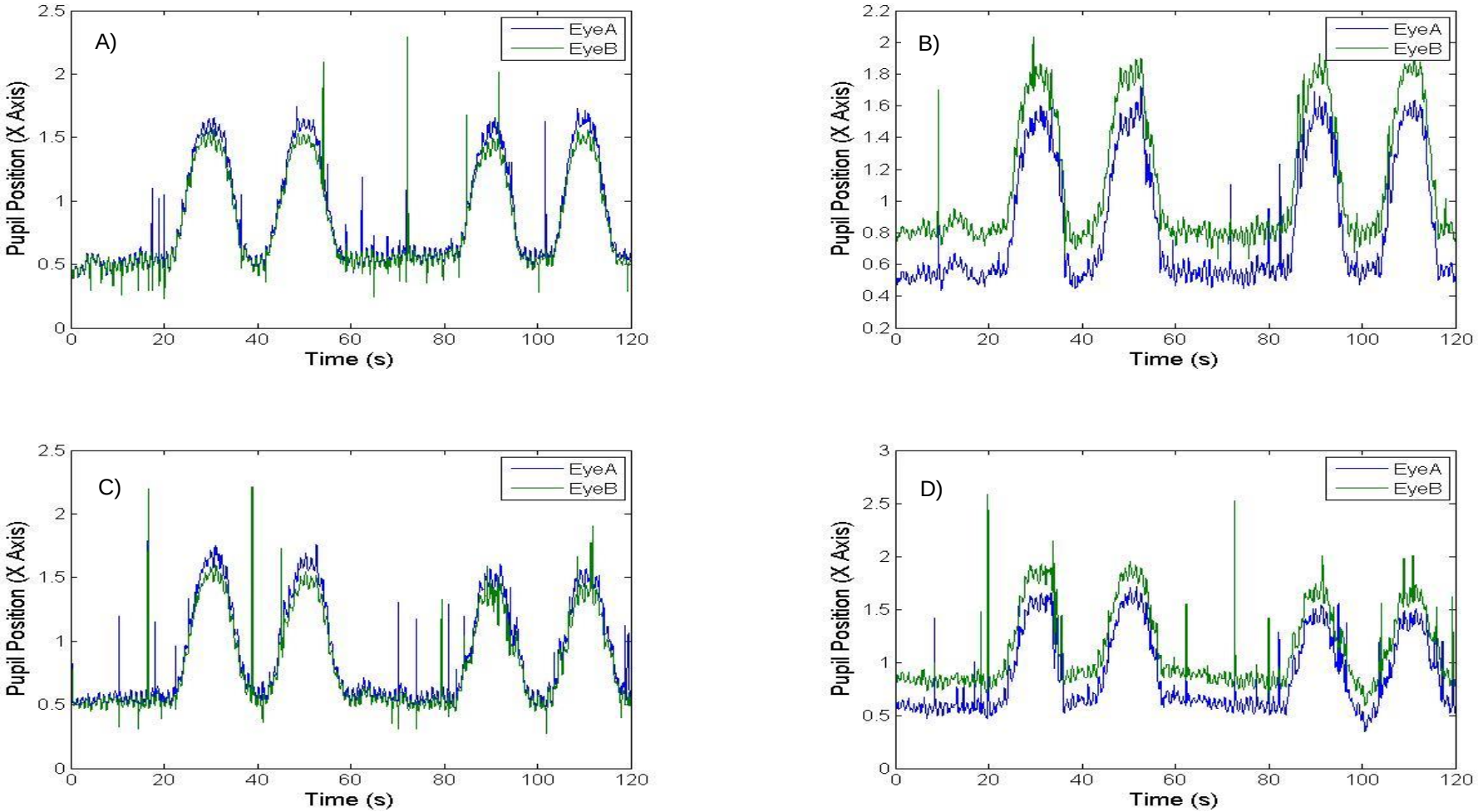




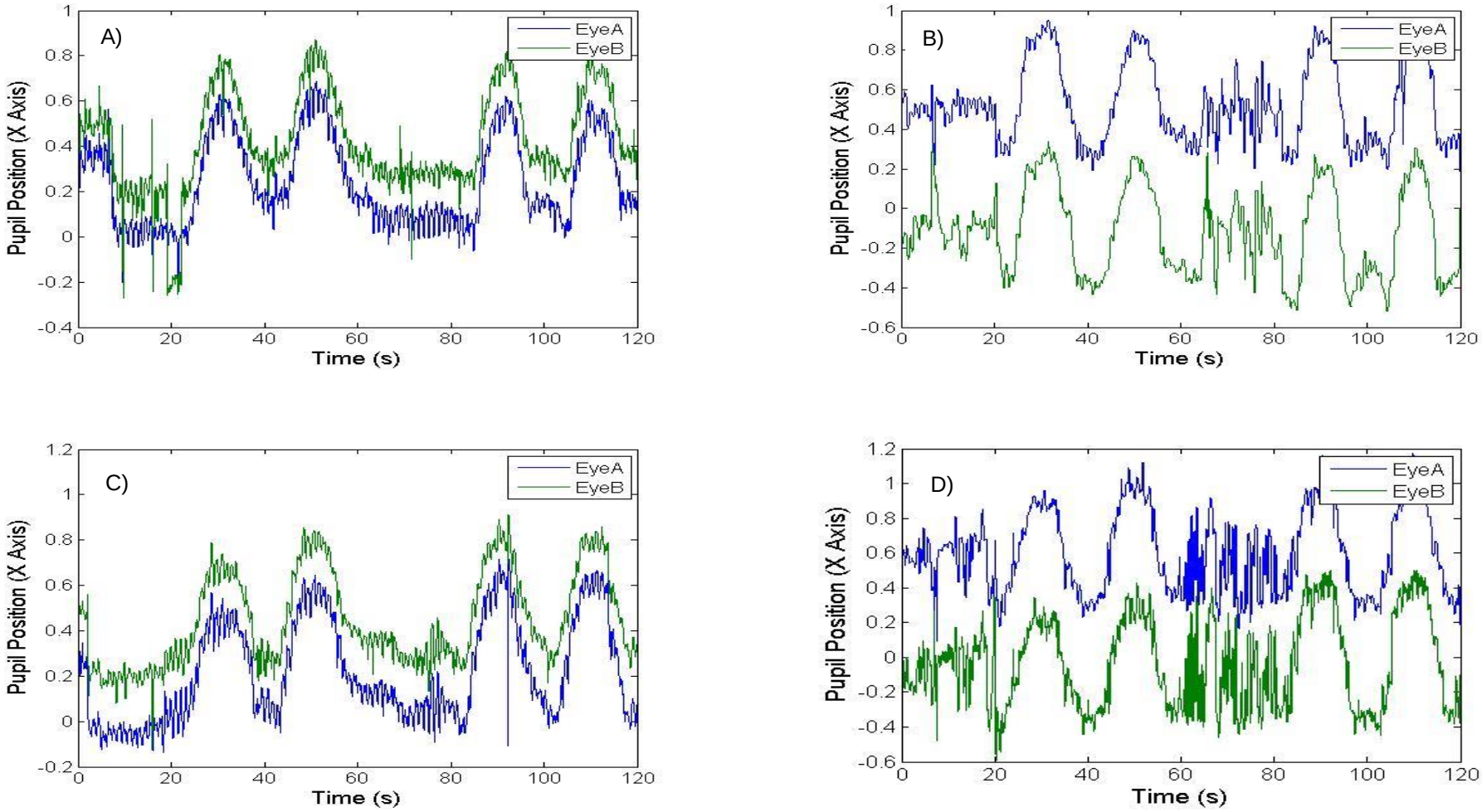
Appendix A2.20: Diagrammatic comparison of the range of foot pressure MSE during (A) Gaze fixation vs Smooth Pursuit on the blank background, and (B) Smooth Pursuit across the three backgrounds for subject 10.

Appendix 3: Supplementary Information for Chapter 4

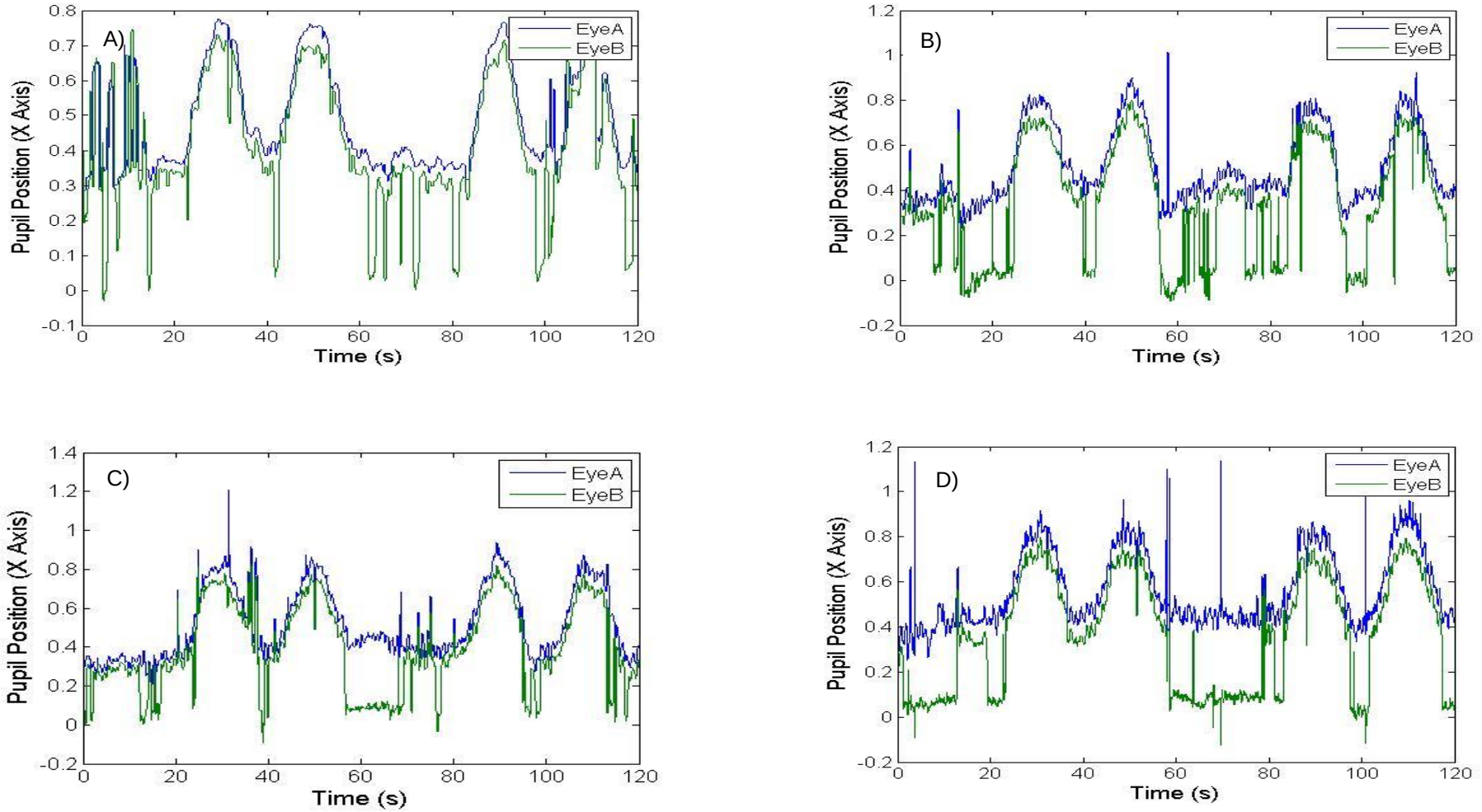
This Appendix includes Eye Tracking and Foot Pressure mean square profiles associated with Chapter 4.



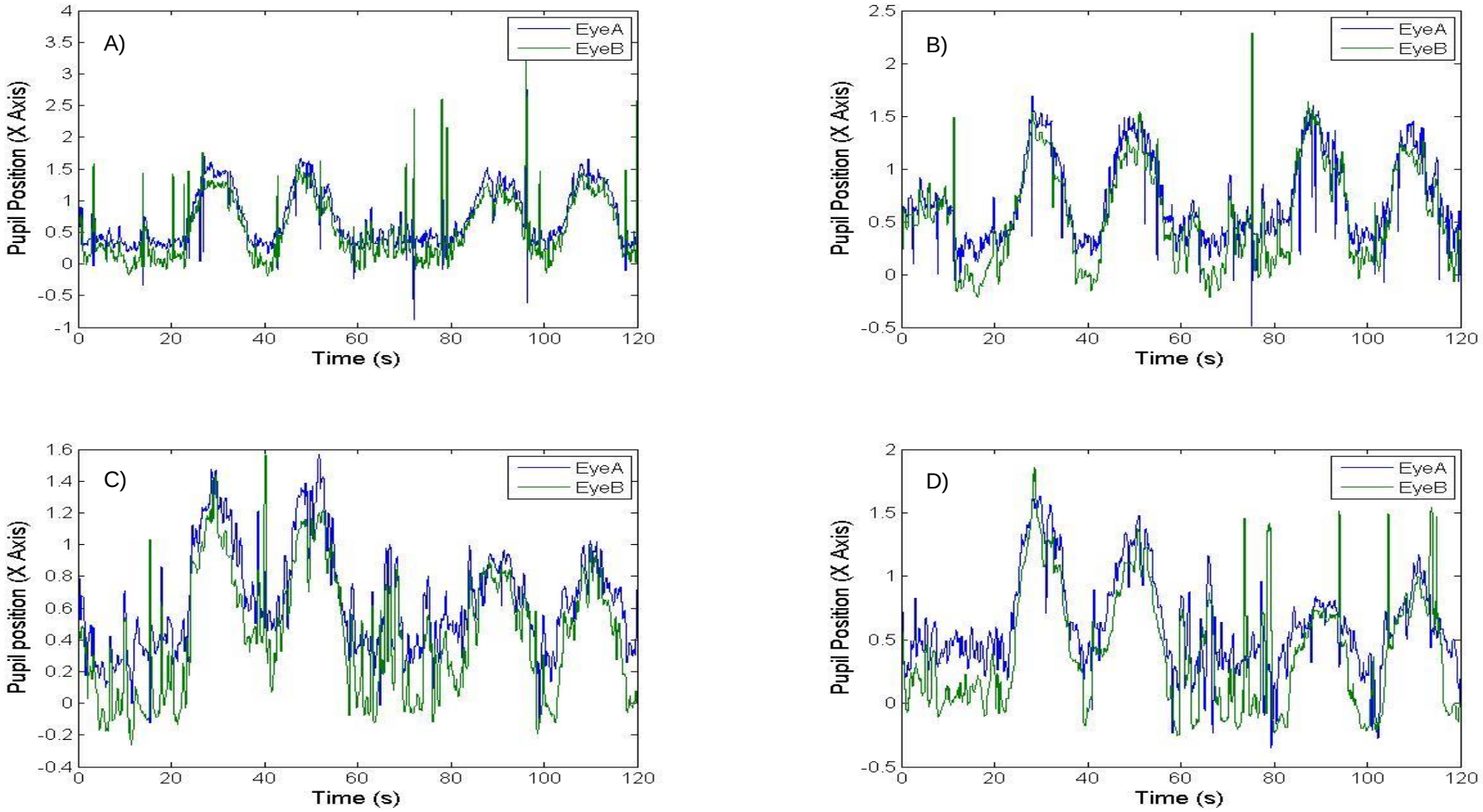
Appendix A3.1: Subject 1 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.



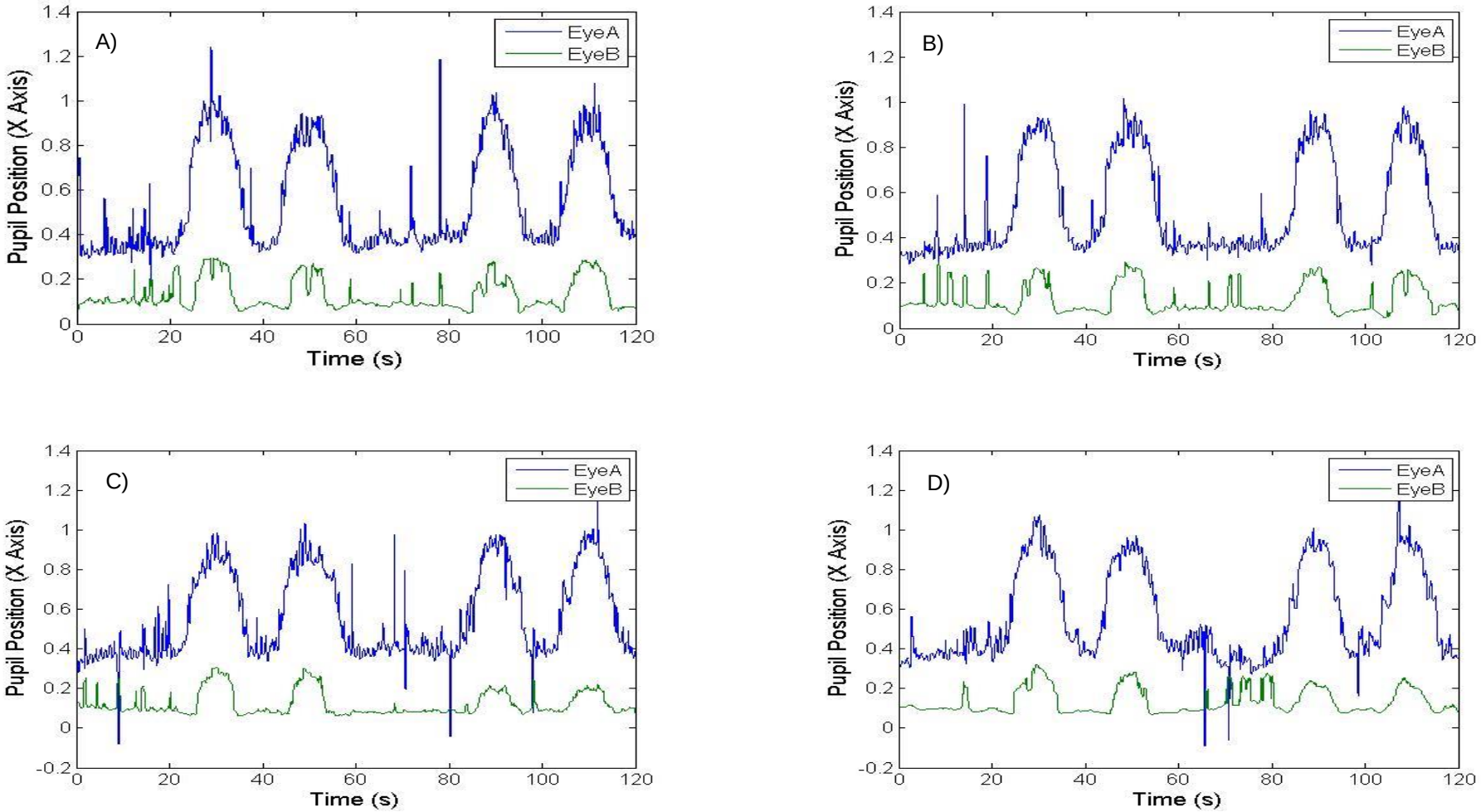
Appendix A3.2: Subject 2 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.



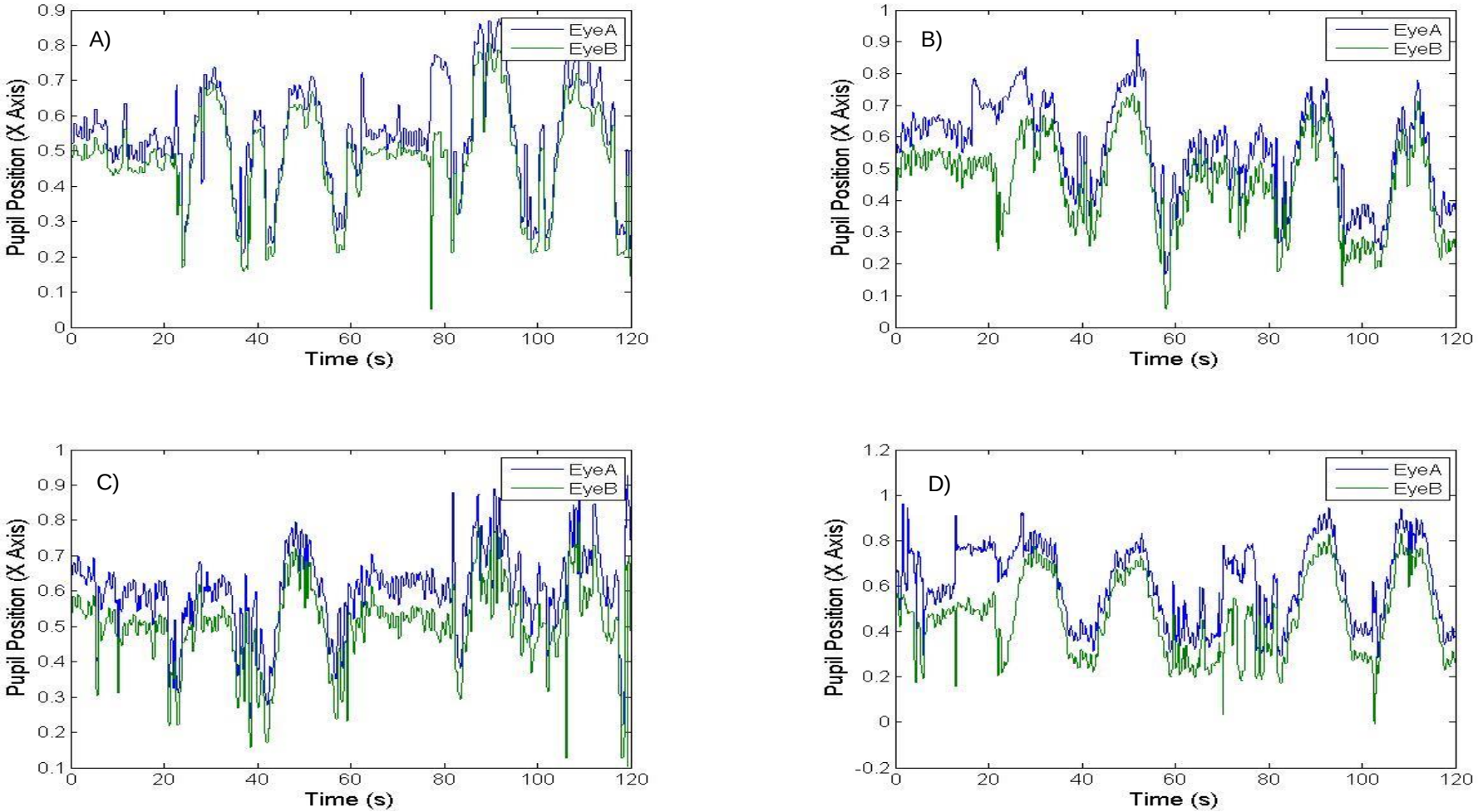
Appendix A3.3: Subject 3 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.



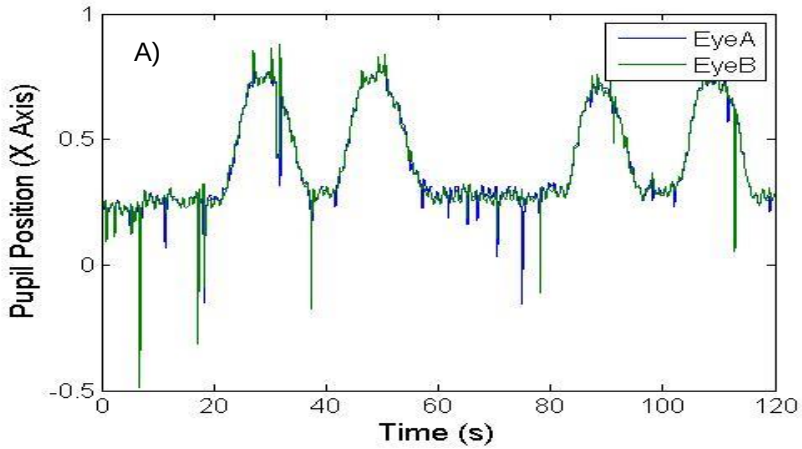
Appendix A3.4: Subject 4 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.

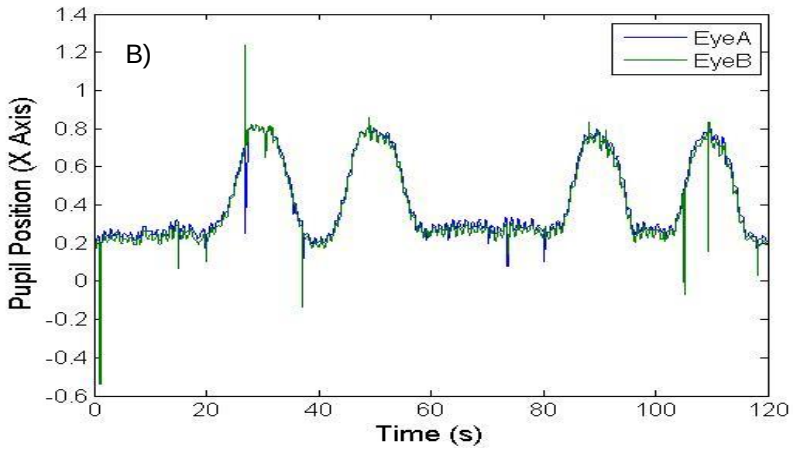


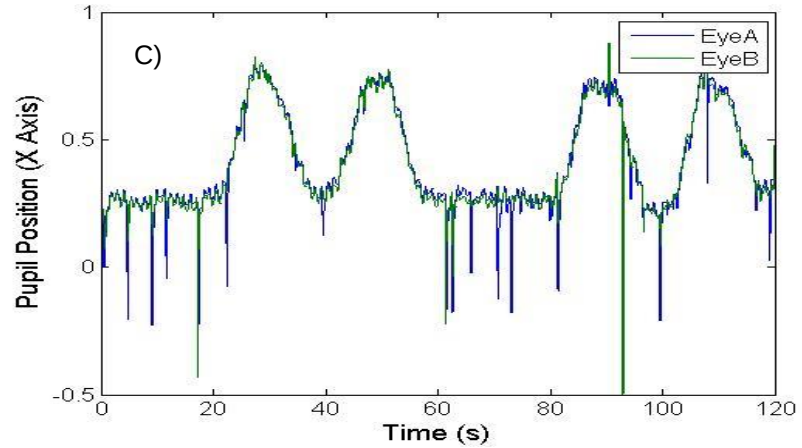
Appendix A3.5: Subject 5 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.

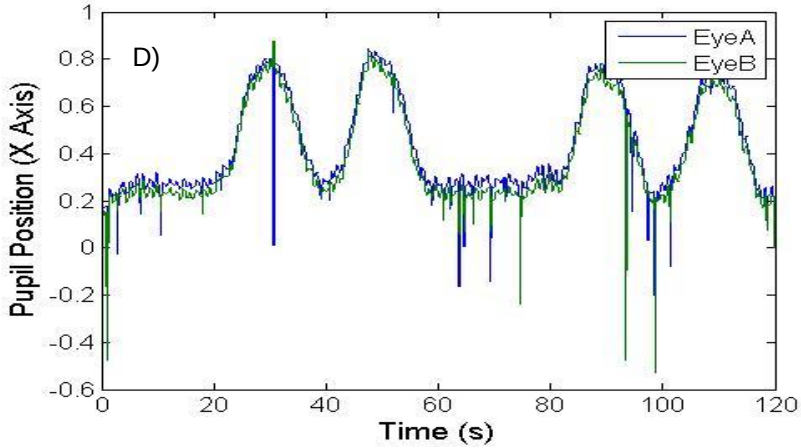


Appendix A3.6: Subject 6 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.

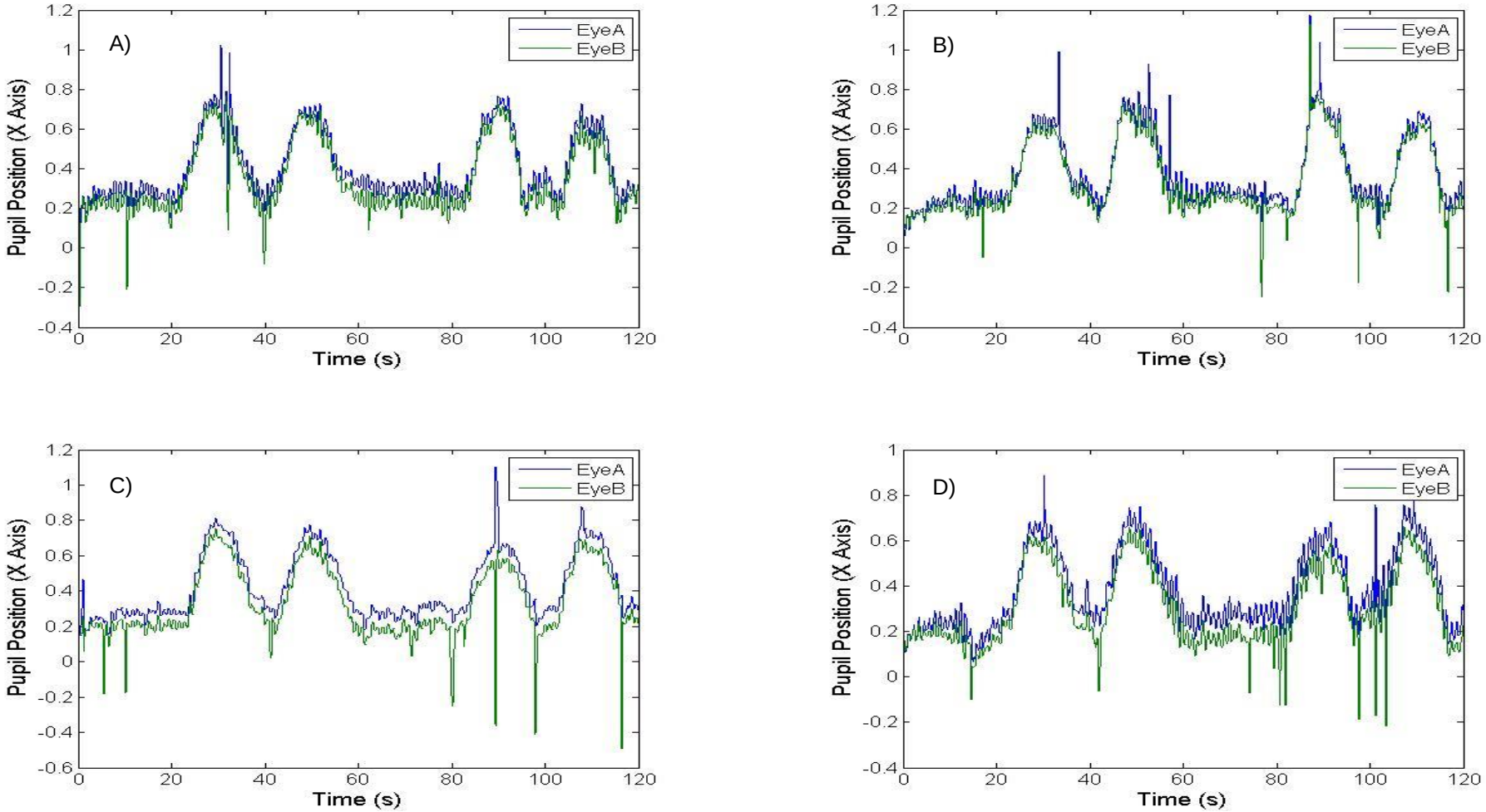




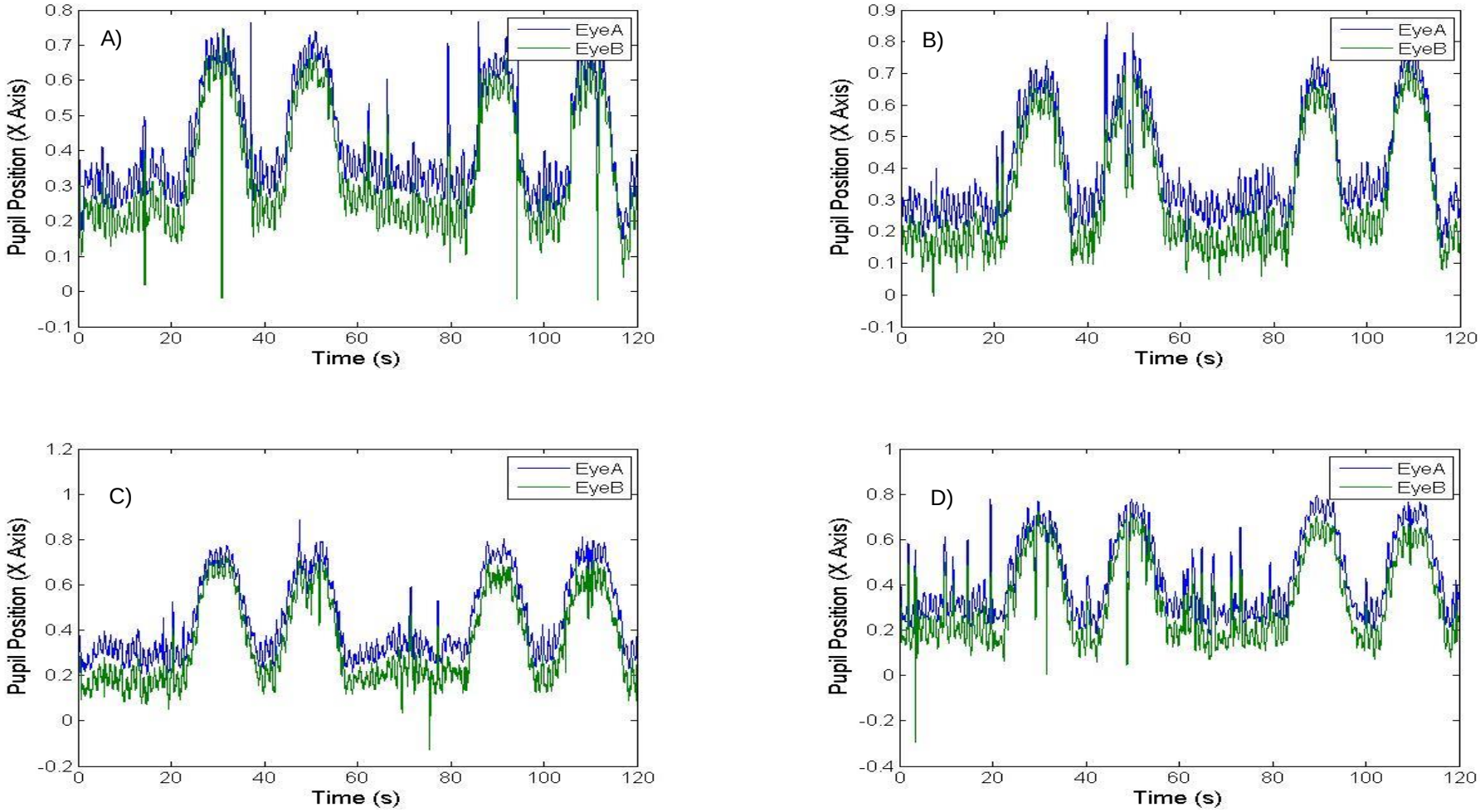




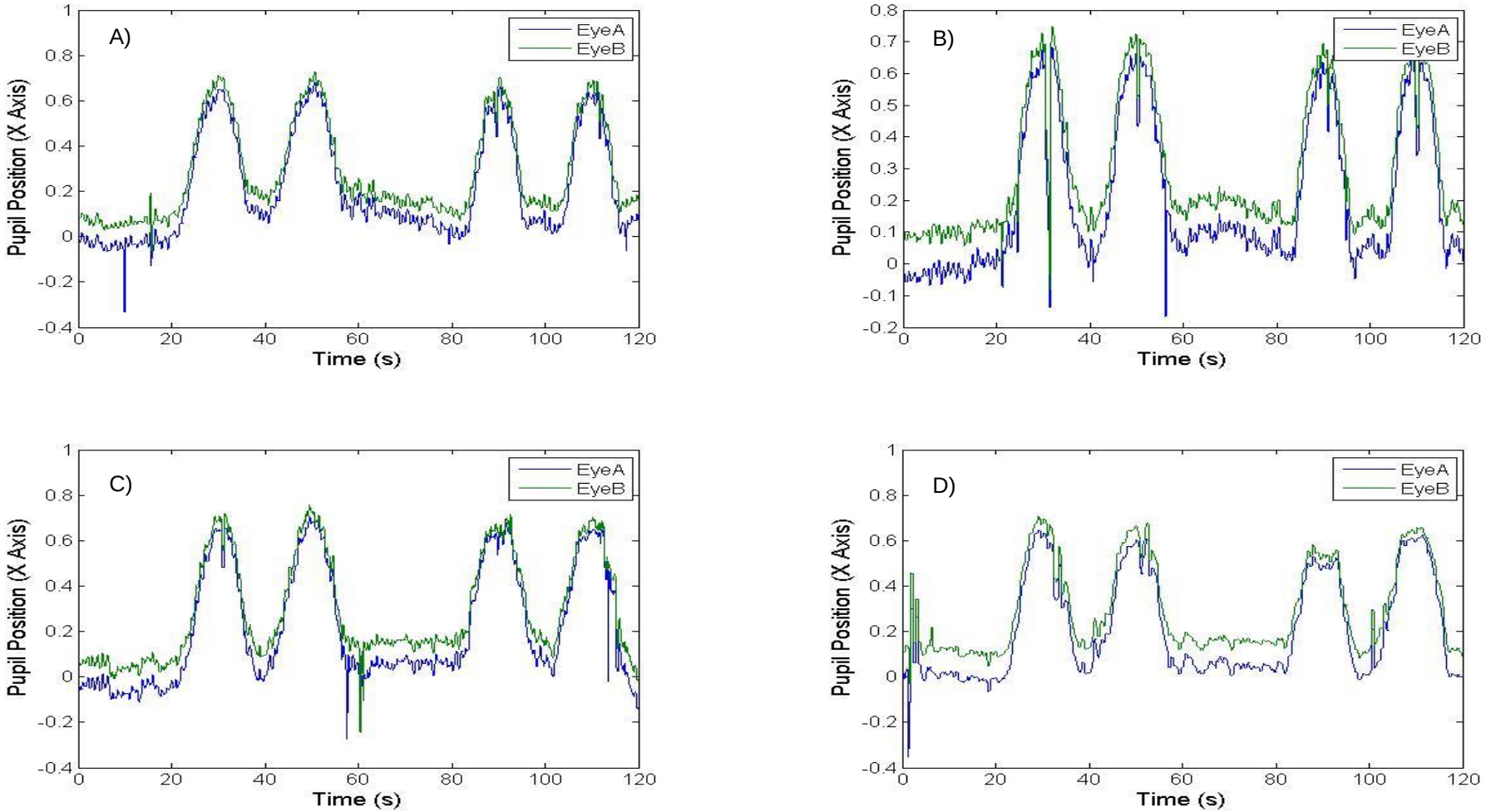
Appendix A3.7: Subject 7 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.



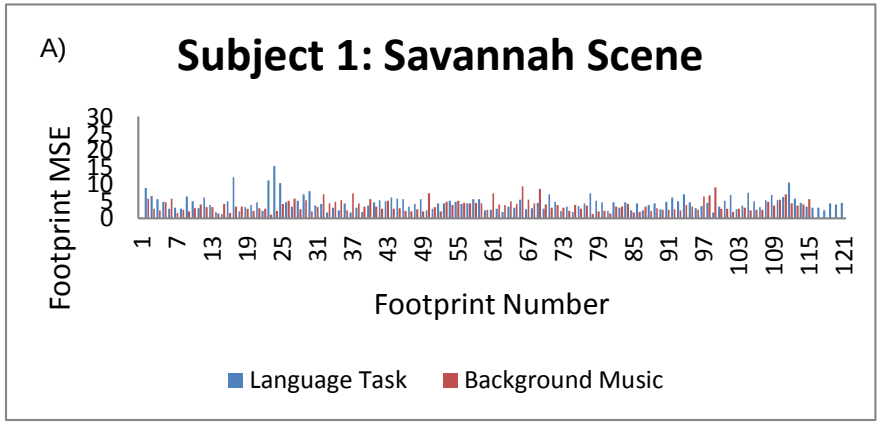
Appendix A3.8: Subject 8 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.

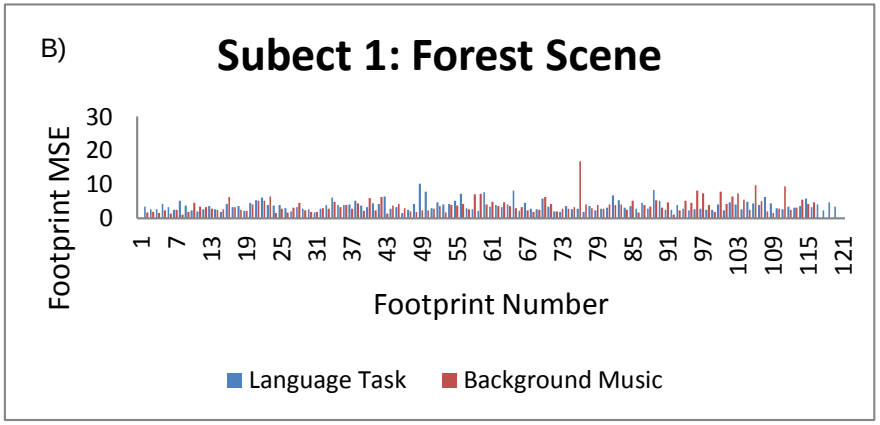


Appendix A3.9: Subject 9 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.

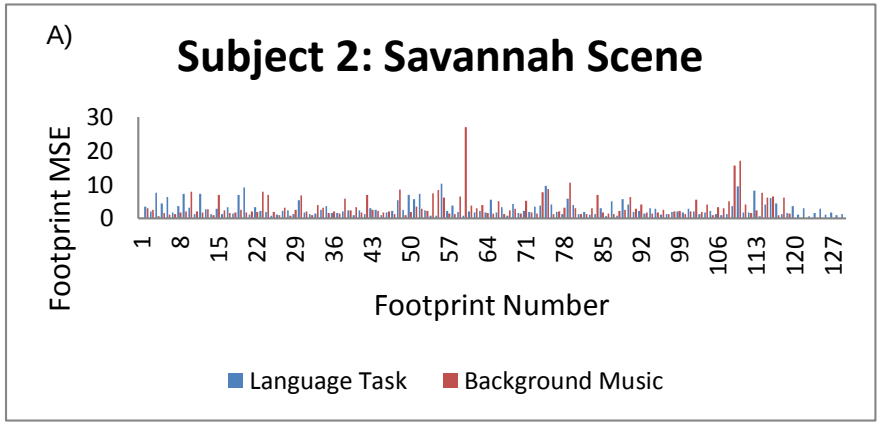


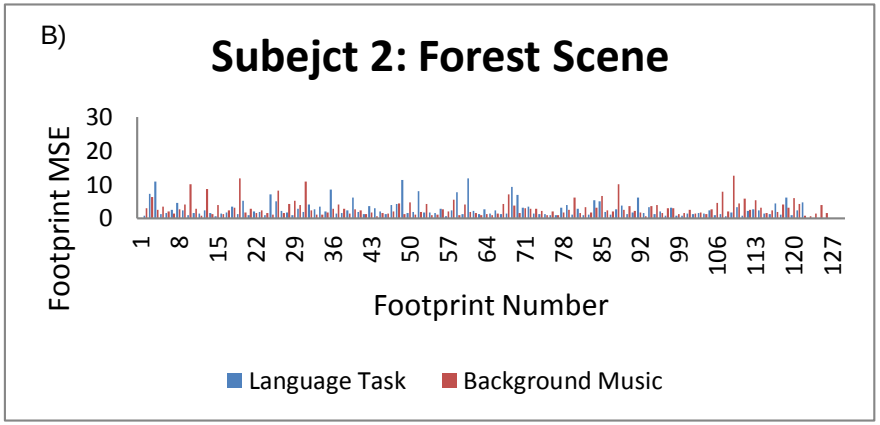
Appendix A3.10: Subject 10 eye tracking profiles for dual task study. A) Repeat back language task when object tracking on the savannah scene. B) Background music task when object tracking on the savannah scene. C) Repeat back language task when object tracking on the forest scene. D) Background music task when object tracking on the forest scene.



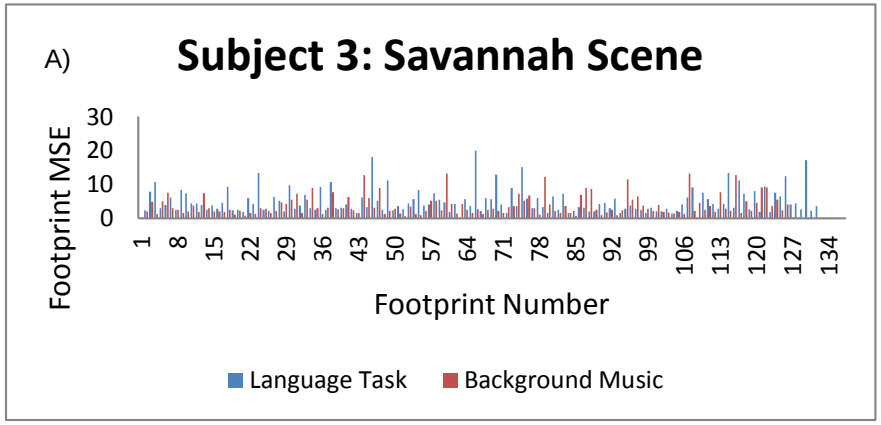


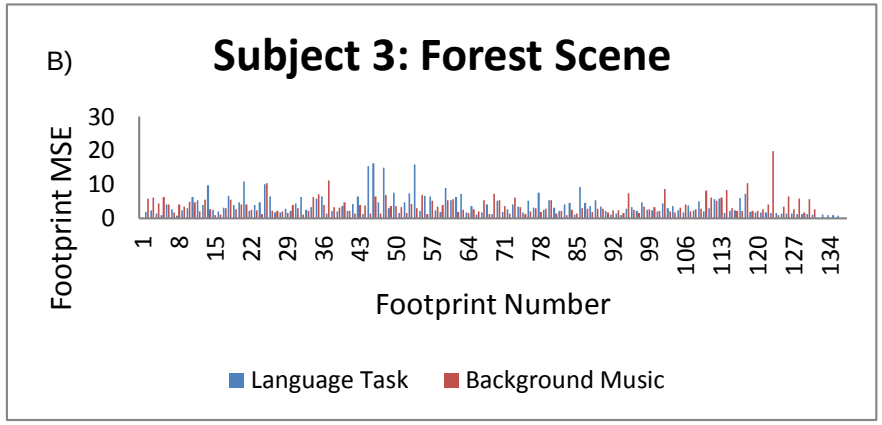
Appendix A3.11: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 1. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.



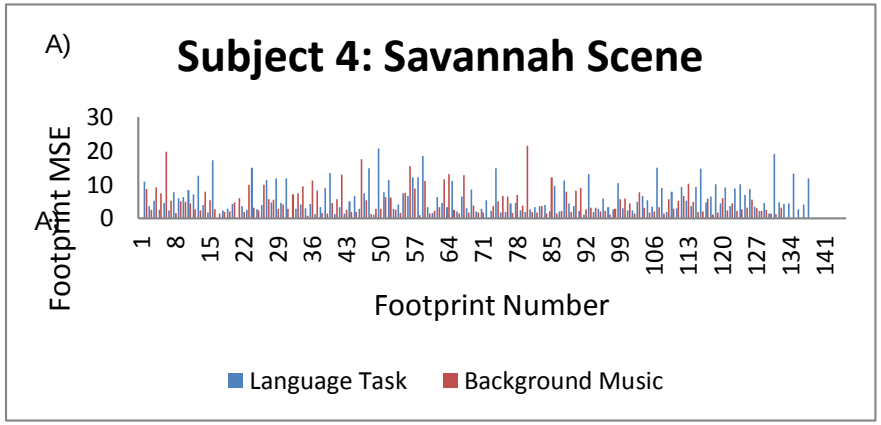


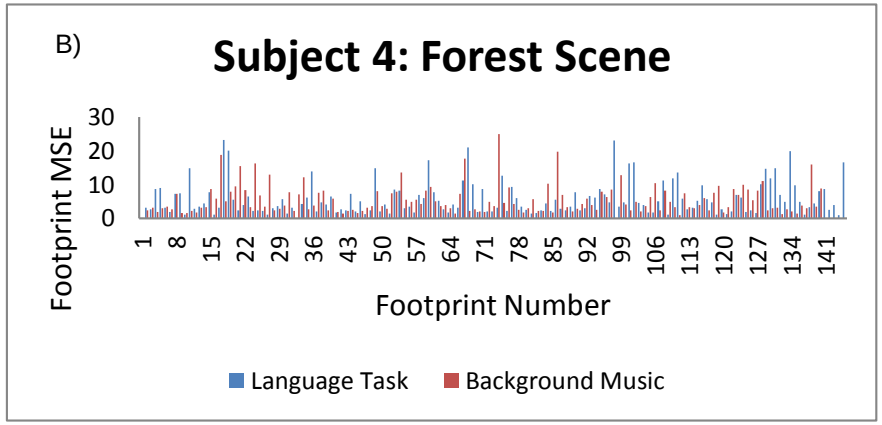
Appendix A3.12: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 2. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.



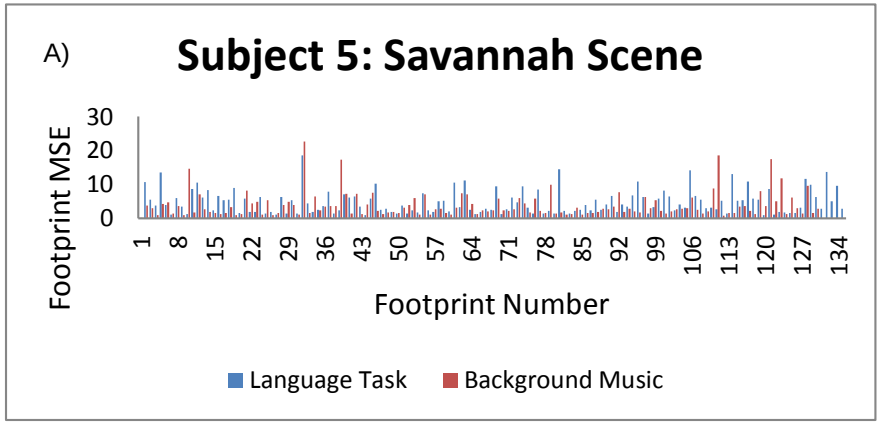


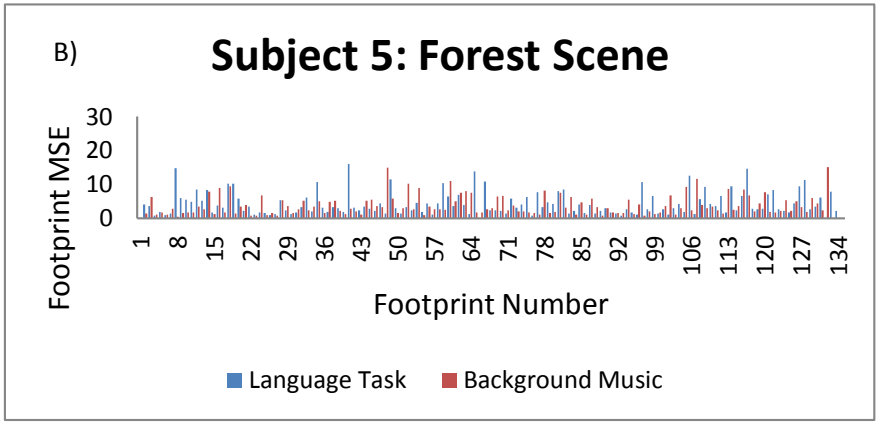
Appendix A3.13: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 3. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.



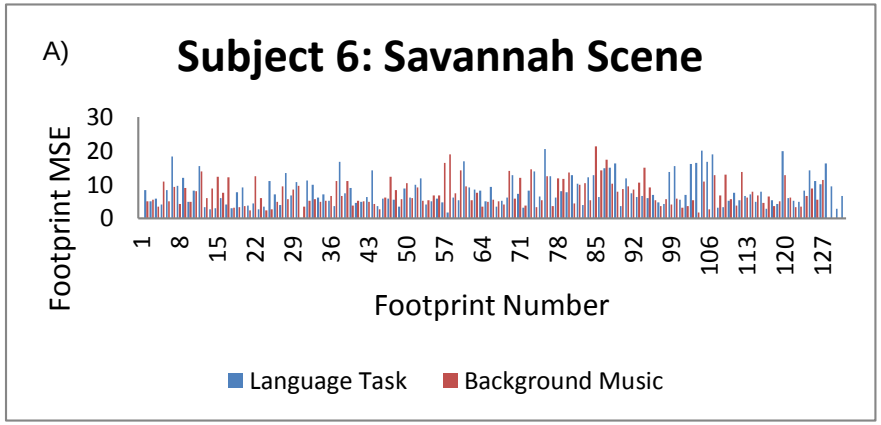


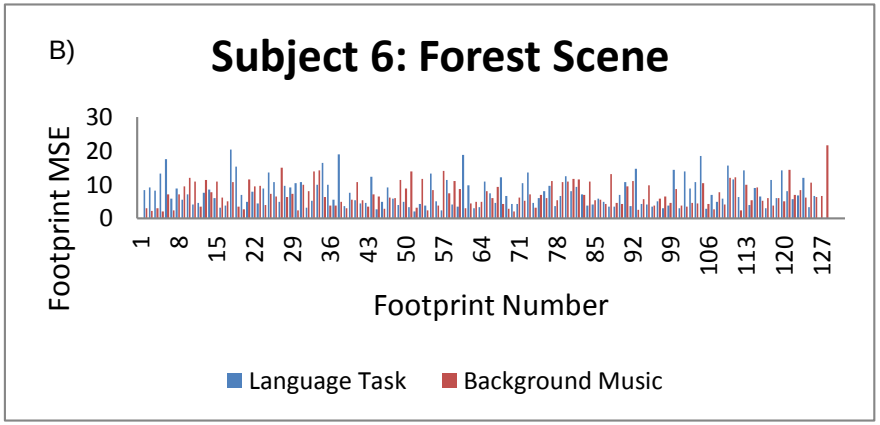
Appendix A3.14: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 4. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.



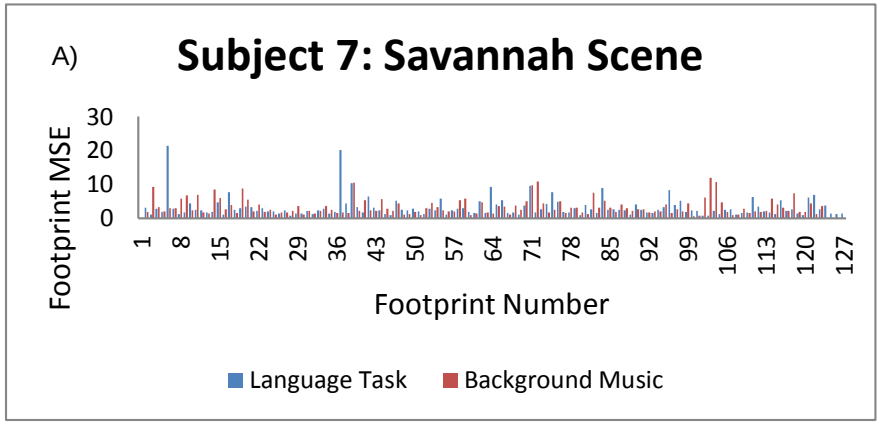


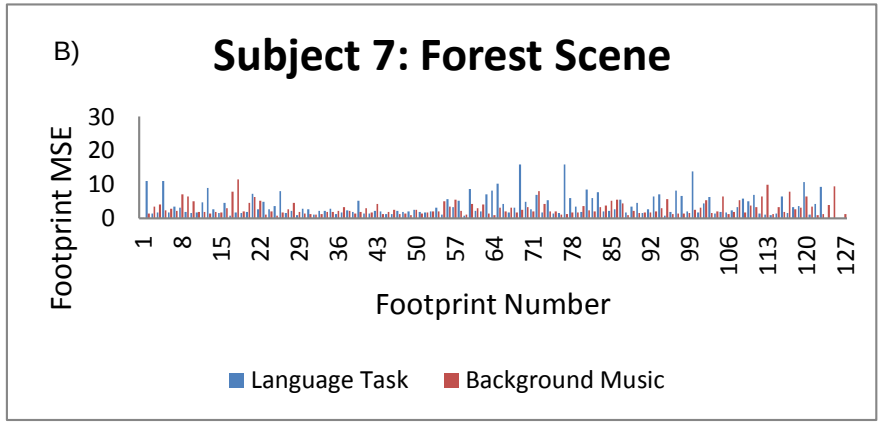
Appendix A3.15: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 5. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.



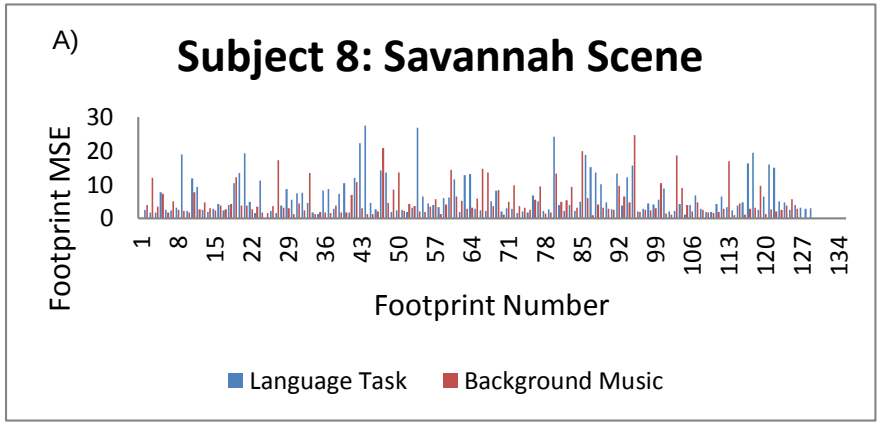


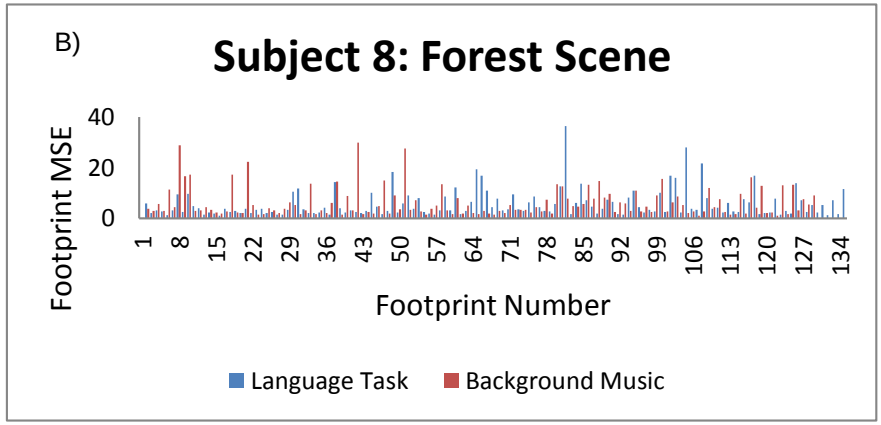
Appendix A3.16: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 6. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.



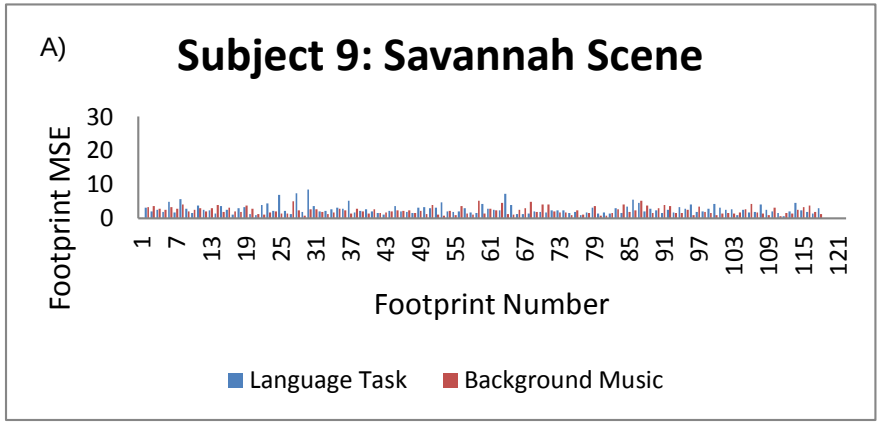


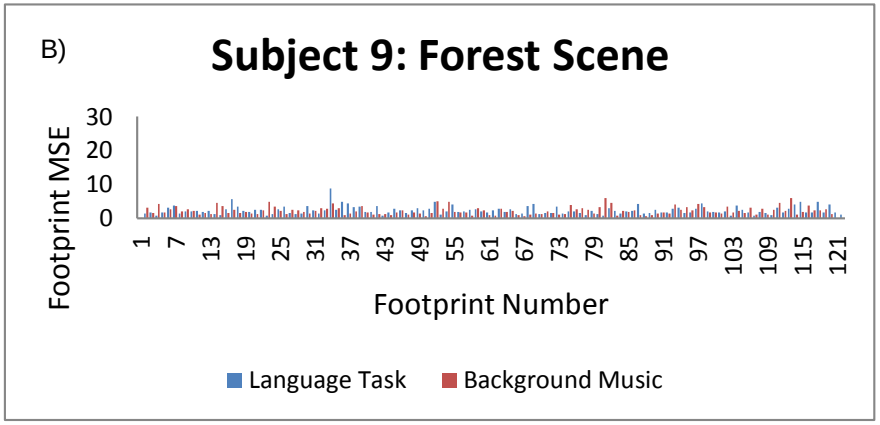
Appendix A3.17: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 7. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.



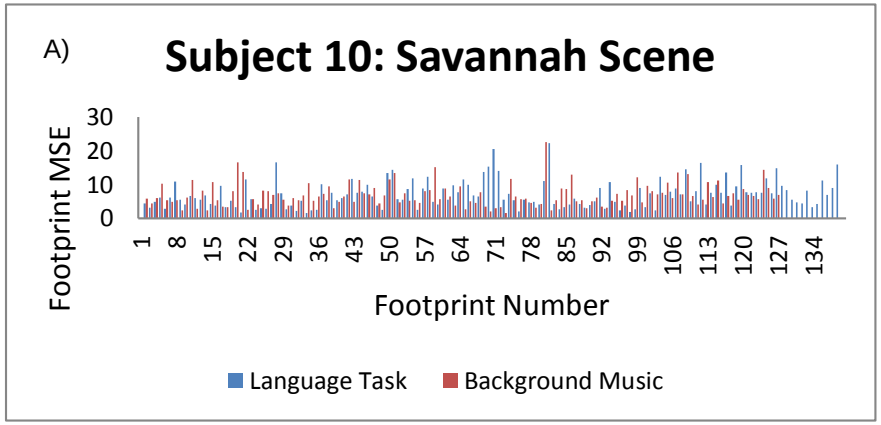


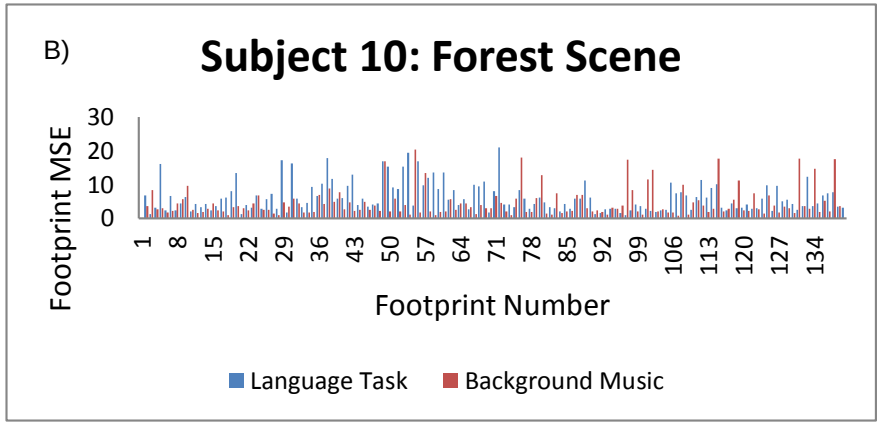
Appendix A3.18: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 8. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.





Appendix A3.19: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 9. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.

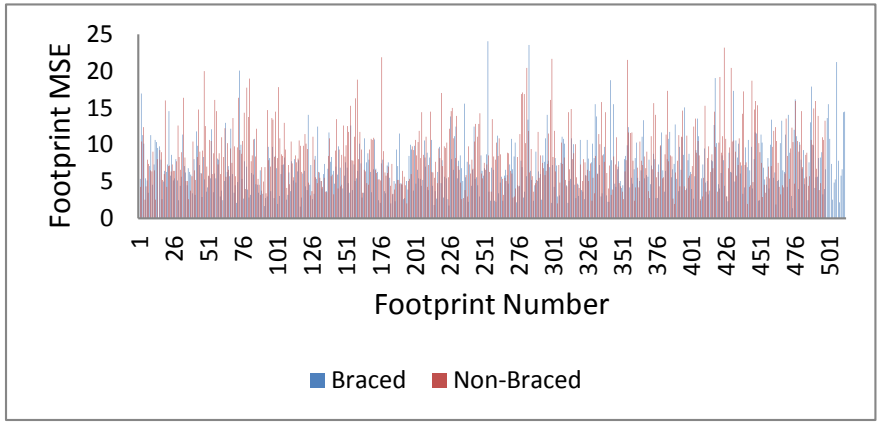




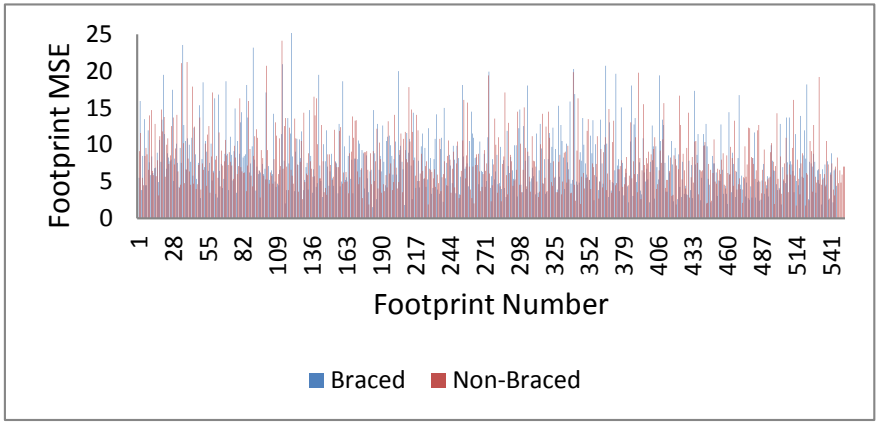
Appendix A3.20: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 10. A) dual tasking in the presence of the savannah scene. B) dual tasking in the presence of the forest scene.

Appendix 4: Supplementary Information for Chapter 5

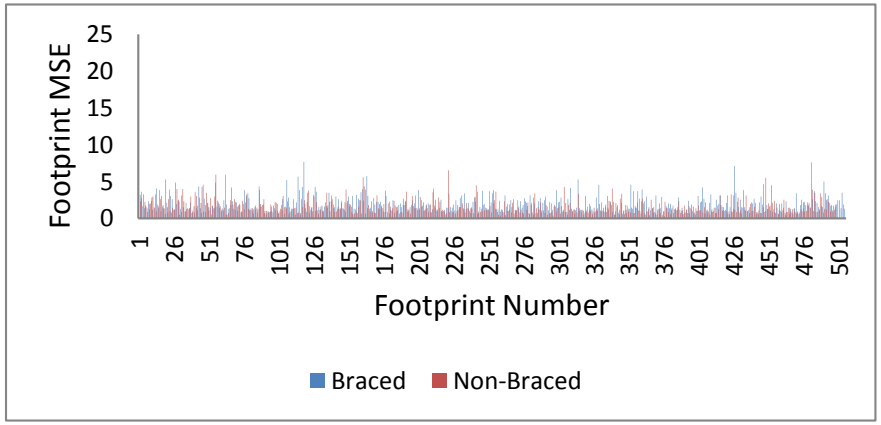
This Appendix presents Foot Pressure MSE profiles associated with Chapter 5.



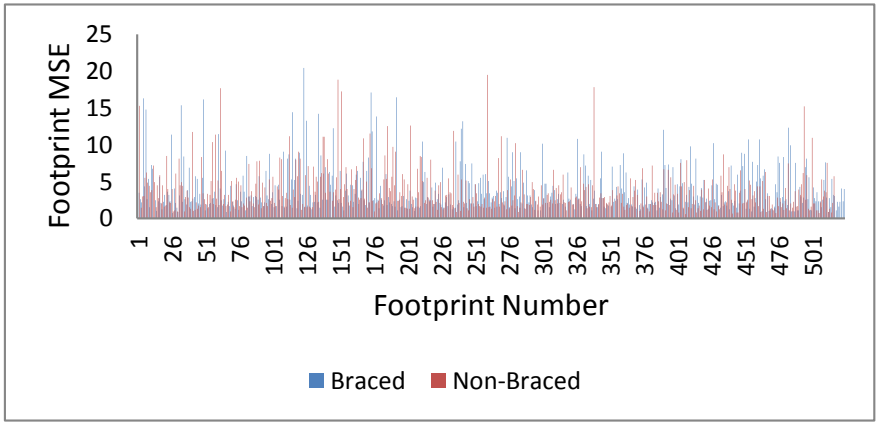
Appendix A4.1: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 1.



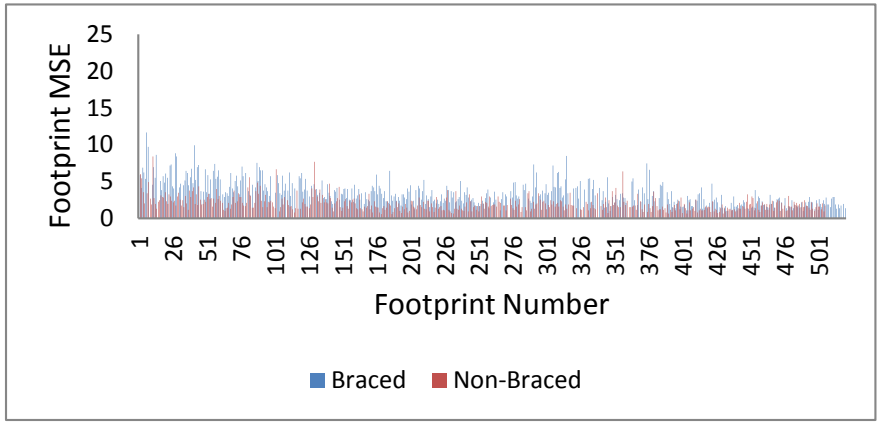
Appendix A4.2: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 2.



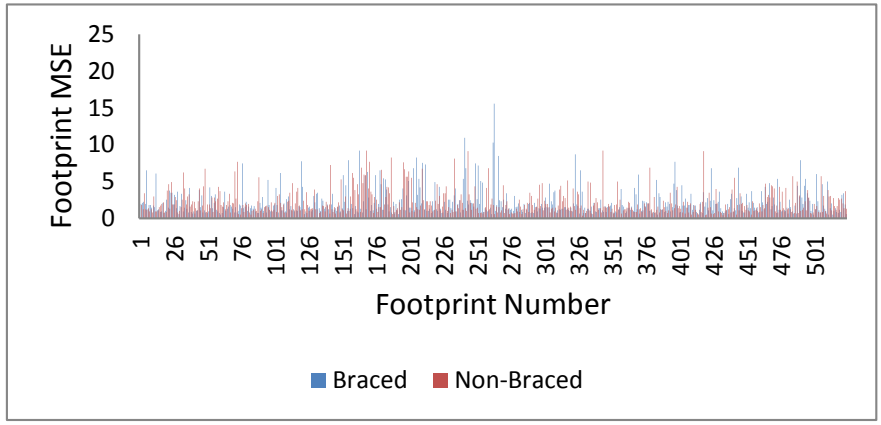
Appendix A4.3: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 3.



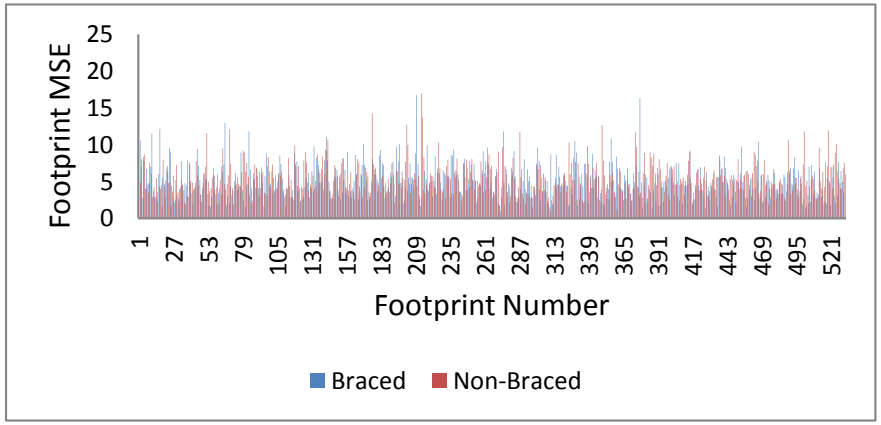
Appendix A4.4: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 4.



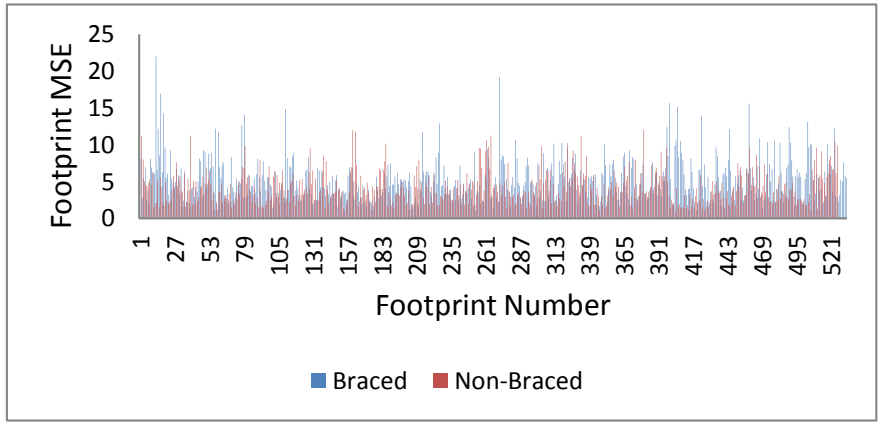
Appendix A4.5: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 5.



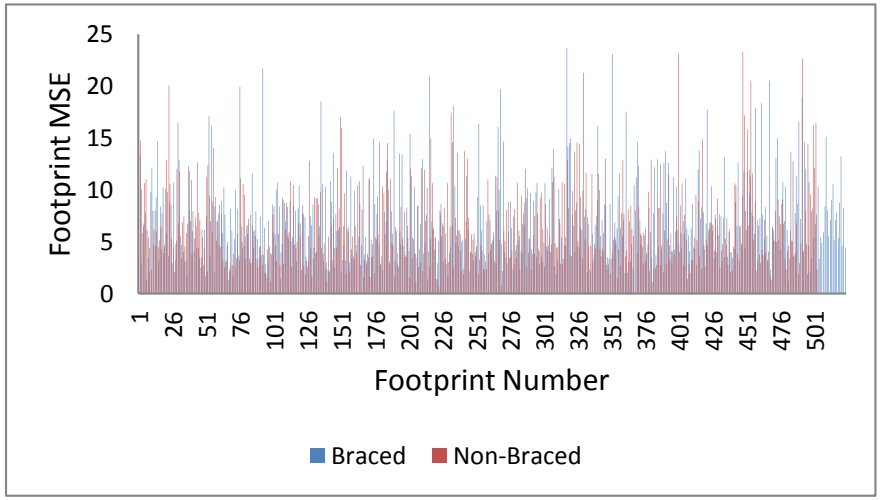
Appendix A4.6: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 6.



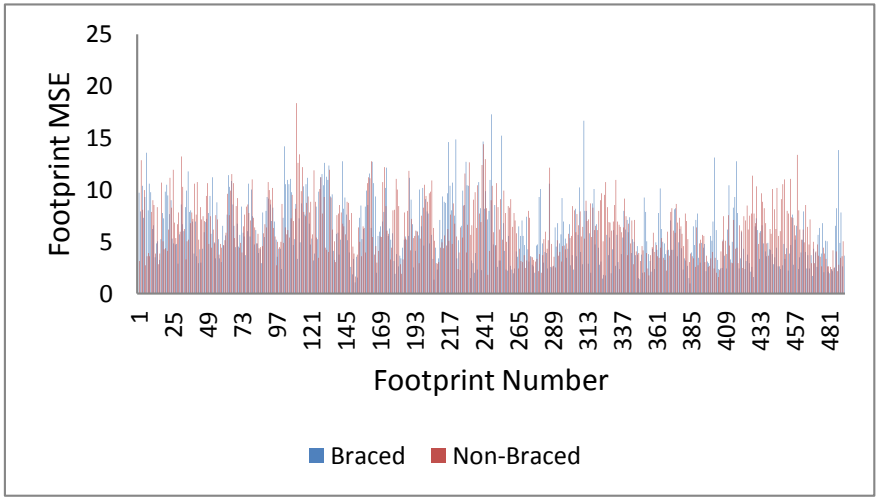
Appendix A4.7: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 7.



Appendix A4.8: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 8.



Appendix A4.9: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 9.



Appendix A4.10: Diagrammatic comparisons of MSE values for individual foot pressure records during each dual task condition for subject 10.

Appendix 5: Publications

Webster E, Hudson P, Channon S. 2014 'Comparative Functional Anatomy of the Epaxial Musculature of Dogs (*Canis familiaris*) bred for Sprinting versus Fighting'. *J Anat.* doi: 10.1111/joa.12208

Bates KT, Collins D, Savage R, McClymont J, **Webster E**, Pataky TC, D'Aout K, Sellers WI, Bennett MR, Crompton RH. 2013 'The evolution of compliance in the human lateral mid-foot.' *Proc R Soc B* 280: 20131818.

Bates KT, Savage R, Pataky TC, Morse SA, **Webster E**, Falkingham PL, Ren L, Qian Z, Collins D, Bennett MR, McClymont J, Crompton RH. 2013 'Does footprint depth correlate with foot motion and pressure?' *J R Soc Interface* 10: 20130009.